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PHYTOPLANKTON PHOTOSYNTHESIS IN SANCTUARY LAKE, PYMATUNING RESERVOIR

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One of the basic factors governing the biological productivity of a lake is photosynthesis. It represents the underlying process on which depends the production of organic material. Many workers have recognized its significance and some (Manning and Juday 1941) (Gessner 1949) have developed criteria of productivity by measuring photosynthetic rates per unit of chlorophyll in the water. These workers assumed that once they had established an average rate for a few lakes, they could apply this rate to other lakes in which they made no measurements of photosynthesis, but simply estimated the amount of chlorophyll present. Their criterion would seem to be one of the best yet devised for roughly comparing the primary productivity of different lakes. However, much remains to be learned concerning variations in photosynthetic rates in relation to time, from one lake to another and among natural communities of different phytoplankton species. In the present investigation, photosynthetic and respiratory rates of the Myxophycean communities in Sanctuary Lake were studied during the summer of 1951. The rates observed are described and discussed below.

The authors would like to acknowledge advice and guidance for this investigation from Dr. Jacob Verduin of the Franz Theodore Stone Institute of Hydrobiology. The equipment used in this study was provided by the Pymatuning Laboratory, University of Pittsburgh.

METHODS

A method of measuring the photosynthetic yield of phytoplankton has been described by Verduin (1951). In this method, the pH change occurring during a test period is used to determine carbon dioxide removed during photosynthesis or evolved during respiration. The equilibrium equations and graphs published by Moore (1939) and nomographs by Dye (1944) provide the basis for such measurements.

During the summer of 1951, this method for measuring photosynthetic rates was employed in Sanctuary Lake, the uppermost division of Pymatuning Reservoir near Linesville, Pa. This lake supports such dense phytoplankton populations that they can be studied without concentrating the natural population (Tryon and Jackson 1952). The average ash-free dry weight obtained in the summer of 1951 was 18.9 mg. per liter. Because of this heavy population, it was possible to study rates under more nearly natural conditions than has been done heretofore.

Estimates of photosynthetic yield were made in two ways: (1) by measuring the pH change occurring in bottles submerged in the lake and (2) by the measurement of pH change occurring under natural conditions in the lake. The procedure in (1) consisted of collecting a liter of lake water, measuring pH and total alkalinity and putting aliquot portions into bottles which had been arranged in pairs at measured distances along a chain. Because of the heavy phytoplankton population and because of the shallowness of the lake (mean depth approximately 5 feet), the following depths were chosen: surface, 6″, 9″, 12″, 15″, 18″, 24″. Two light-proof bottles were placed at the 30″ mark. These were used in determining respiration. The apparatus was suspended in the lake for 3 or 4 hour periods. At the end of the time interval, the bottles were removed and the pH of each was measured immediately with a Beckman pH meter.

Figure 1 shows graphically the relation between pH change and carbon dioxide change in Sanctuary Lake, which has an alkalinity of 53 ppm. This graph was constructed with the aid of nomographs (Dye 1944). The steep slope of the curve at low pH values primarily represents changes in free CO_2. The flat portion of the curve represents changes in half-bound CO_2. It is not unusual for the pH in Sanctuary Lake to change from 7.2 to 9.2 in a single day.

Table I shows data from Sanctuary Lake for August 17 during the interval from 0800 to 1200,

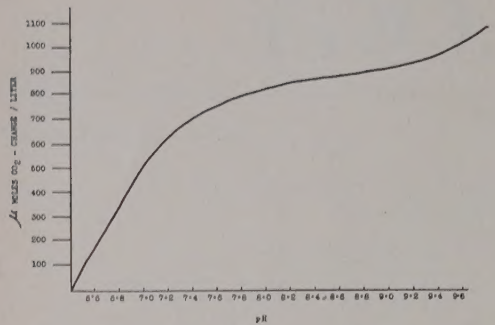

FIG. 1. Relationship of CO_2 removal to pH change between the values of 6.6 to 9.6, with total alkalinity of 53 ppm.

using the suspended bottle technique. The pH of the water at 0800 before it was put in the bottles was 7.42. At the end of the four hour period, the pH of the water in the surface bottle had risen to 8.37. This rise in pH resulted from the utilization of 90μ moles of carbon dioxide, as indicated by Figure 1. This amount of carbon dioxide was utilized by 20.5 mg. ash-free dry weight of plankton in four hours. Thus, the apparent photosynthesis was 1.10μ moles CO_2 absorbed per mg. ash-free dry weight per hour. The same procedure was followed for each depth. The black bottles (BB) were used to determine the respiration rate. The carbon dioxide evolved by plankton respiration must be added to apparent photosynthesis to obtain the total rate. The total rates at the various depths were then averaged to give the mean rate of photosynthesis for a 24 inch water column.

TABLE I. *Average hourly rate of total photosynthesis for a 24" water column as obtained by the suspended bottle method*

Depth in inches	pH in bottles	Total photosynthesis μ moles CO2/mg. ash-free dry wt./hour
8	8.37	1.47
6	8.32	1.47
9	8.05	1.16
12	7.81	.92
15	7.77	.86
18	7.66	.80
24	7.39	.31
BB	7.29	...
		Average 1.00

For the measurement under natural conditions, the pH of Sanctuary Lake was determined at two hour intervals over a 24 hour period. The calculations were the same as with the submerged bottles. An hourly rate of apparent photosynthesis was computed for the hours of 0800 to 1600. The hourly respiration rate was similarly determined from the night time hours of 2200 to 0600. The sum of these two rates yielded the average rate of total photosynthesis per hour under natural conditions (Table II). The transition period, 1600 to 2200, was not used in calculating photosynthesis or respiration, since light was highly variable during this interval. The negative values represent the condition when respiration exceeded photosynthesis. These values may be considered to represent negative apparent photosynthesis.

TABLE II. *Hourly rates of apparent photosynthesis between initial and final pH values as obtained under natural conditions*

Time	Initial pH	Final pH	Apparent photosynthesis μ moles CO2/mg. ash-free dry wt./hour
0800-1000	7.42	7.48	.24
1000-1200	7.48	7.55	.24
1200-1400	7.55	7.80	.49
1400-1600	7.80	8.12	.73
1600-1800	8.12	8.21	.24
1800-2000	8.21	8.21	0
2000 2200	8.21	8.04	−.37
2200-2400	8.04	7.62	−.85
2400-0200	7.62	7.55	−.24
0200-0400	7.55	7.45	−.37
0400-0600	7.45	7.41	−.12

PHOTOSYNTHETIC RATES

Table III shows the average total photosynthetic yield for the two foot water column in which the bottles were suspended. This table shows 9 tests, each made during the afternoon of nine separate days. The average rate for the 9 tests was 1.34μ moles CO_2 absorbed per mg. ash free dry weight per hour. The first three figures represent a *Microcystis-Anabaena* community, the next three figures show almost pure stands of *Microcystis,* the next two are a *Microcystis-Aphanizomenon* community, and the last a *Microcystis-Aphanizomenon-Anabaena* community. The rates observed were variable, the highest value was more than twice the lowest, but no significant difference between rates of different communities was established. This observation seems to support Verduin's (1951) conclusions from Lake Erie studies, namely, "that the major components of the communities which are adapted to a particular aquatic habitat exhibit closely similar photosynthetic rates per unit of plant volume." In this investigation, however, the rates are based on ash-free dry weight, not on plant volume.

Table IV shows the average photosynthetic rate obtained from 4 tests under natural condi-

TABLE III. *Average hourly rates of total photosynthesis of three phytoplankton communities as obtained by the suspended bottle method*

Date	Phytoplankton per cent composition			Total photosynthesis μ moles CO2/mg. ash-free dry wt./hour
	Microcystis	*Aphanizomenon*	*Anabaena*	
6-28....	80	0	15	1.22
6-29....	80	0	15	1.27
6-30....	90	0	10	2.25
7-10....	95	0	0	1.49
7-12....	95	0	0	.90
7-14....	95	0	0	1.08
7-28....	70	30	0	1.01
8-4.....	15	80	0	1.64
8-17....	40	50	5	1.22

tions, which gives a figure of 1.00μ moles CO_2 absorbed per mg. ash-free dry weight per hour.

TABLE IV. *Average hourly rates of total photosynthesis as obtained under natural conditions*

Date	Total photosynthesis μ moles CO2/mg. ash free-dry wt./hour
7-14.....	1.38
7-28.....	1.00
8-4.....	.80
8-17.....	.82

This agrees within about 75 per cent with that obtained from the submerged bottles, in spite of such sources of error as water mass movements, CO_2 absorption from air, and the use of a night respiration rate for correcting apparent photosynthesis by day. The fairly close agreement between the two estimates suggests that the phytoplankton enclosed in bottles are functioning much as they do in their natural environment. What disparity there is between the two estimates may be largely overcome by taking a greater number of samples from different areas of the lake.

Figure 2 shows the course of apparent photosynthesis at two hour intervals on August 17-18. Note the increasing rate from 0800 to 1600. After 1600, the rate decreased. After 2000, respiration plus carbon dioxide absorption from air exceeded photosynthesis. The magnitude of CO_2 absorption from air has not been determined. The striking feature of this graph is the variability it portrays. A rate increase of nearly fourfold between sunrise and 1600, followed by a sharp decrease while light is still abundant, is a most striking phenomenon. Similarly noteworthy is the high respiration rate near midnight, approximating the magnitude of

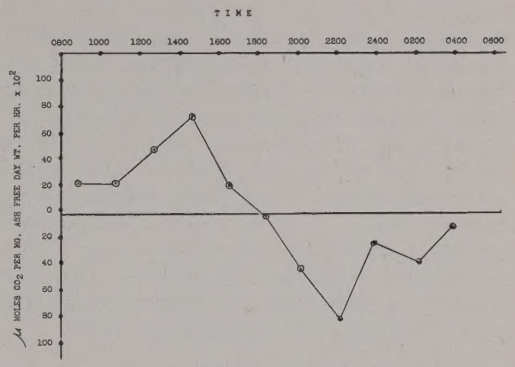

FIG. 2. The course of apparent photosynthesis during a 22 hour period.

the highest apparent photosynthetic rate, followed by decreasing respiration rates during the hours of total darkness.

The area under the daytime curve is approximately the same as the area above the nighttime curve for the same day. This suggests that carbon dioxide replenishment during the dark period is roughly as great as carbon dioxide removal from the water during the light period. If carbon dioxide absorption from air is neglected, this situation would suggest that apparent photosynthesis during the day was only sufficient to provide carbohydrates for night respiration. If this were true, there would be no carbohydrate available for growth. But carbon dioxide absorption from air is not negligible and it may be closely similar to the magnitude of "net photosynthesis," *i.e.*, photosynthesis in excess of respiration during a 24 hour period. Undoubtedly the areas under and over these curves will alter markedly under varying conditions, such as different growth stages in the community. It may be that "net photosynthesis" is high during the growth phase of a community, close to zero at the plateau or even at the inflection point and that "net photosynthesis" may be negative during the decay of a community. These relationships remain to be investigated. Gessner (1949) presents some data containing evidence of such variation, but his sampling frequency was too low to yield conclusive information.

Diurnal variations in respiration rates were observed in the black bottles also. The combined data from black bottles and from studies such as that shown in Figure 2 indicated that the average respiration rates of phytoplankton expressed in μ moles carbon dioxide evolved per mg. ash-free dry weight per hour are: from 0600-1200—.37, from 1200-1800—.62, from 1800-2400—.84 and from 2400-0600—.34. In all the samples, the respiration rates were higher in the earlier part

of the afternoon than in the morning. They were also much higher in early evening (1800-2400) than at any other time in the night. This would seem to indicate that respiration rates increase by day as photosynthesis proceeds and decrease during the latter half of the night. It may be that the gradual increase of photosynthetic rates during the morning hours is associated with increasing respiration rates. In other words, maximum photosynthetic activity is not attained until a high respiration rate has been established. Once the high rate is established, it is maintained into the night hours after photosynthesis has ceased.

Discussion

It would seem that the measurement of photosynthesis by means of change in pH is a practicable and constructive method. It is convenient to handle and can be completed with relative speed. It also makes use largely of portable equipment.

There are many lakes where the daily pH changes are large enough to provide direct estimates of photosynthesis. If studies using pH change are conducted in other lakes, an evaluation may be made as to the use of this method as a criterion of productivity. If rates per mg. ash-free dry weight vary greatly from lake to lake, then primary productivity at least is not closely associated with organic seston. If different lakes are in fairly close agreement, however, then the assumption is rendered more valid.

"Natural" data as to phytoplankton photosynthesis are rather meager. The data in Figure 2 represent a single experiment and other 24 hour periods did not exactly reproduce this curve. The mean photosynthetic rate per mg. ash-free dry weight per hour, however, has been fairly well established and lies in the neighborhood of 1.0-1.3μ moles ash-free dry weight CO_2 per mg. hour. Verduin (1952) obtained a rate of 0.70μ moles CO_2 per mg. hour for an *Asterionella-Cyclotella* community and 0.34 for a *Stephanodiscus* community.

The photosynthetic rates in Sanctuary Lake represent only the upper two foot layer of the water, the remaining three feet below were in practically total darkness. In view of this fact, it is surprising that the agreement between the rates measured in the lake and in the enclosed bottles was so close. It suggests that vertical mixing during the 24 hour run was not extensive since the average photosynthetic activity of a five foot column of water, three feet of which are dark, should be less than half the average for a two foot column.

Many interesting facets of aquatic ecology and physiology may be more easily investigated by the measurement of pH change. One of these possibilities is the study of the respiration rates of aquatic animals. The respiration rates of fishes, aquatic insects or other aquatic invertebrates may be ascertained by measuring the change in pH associated with the liberation of carbon dioxide. Another use of the measurement of pH change is in the investigation of the relationship between phytoplankton production and zooplankton consumption. This may be expressed as the ratio between photosynthesis and respiration. These are only a few of the possibilities open to exploration with this method.

Summary

In this study, photosynthesis and respiration rates of phytoplankton were measured by pH change produced by absorption or evolution of carbon dioxide in water samples from Sanctuary Lake. These samples were obtained during the summer of 1951, when a heavy population of Myxophyceae prevailed. The abundant phytoplankton population in Sanctuary Lake permitted comparable photosynthetic measurements of both the phytoplankton enclosed in bottles suspended in the lake and the identical population occurring simultaneously under natural conditions. The two methods showed close agreement: 1.00μ moles CO_2 absorbed per mg. ash-free dry weight per hour, under strictly natural conditions; 1.34μ moles CO_2 when samples were enclosed in bottles. Respiration rates averaged approximately one-half the total photosynthetic rate, but respiration rates between midnight and noon were significantly lower than rates observed between noon and midnight.

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TRACING FIELD VOLES (*MICROTUS AGRESTIS*) WITH A GEIGER-MÜLLER COUNTER

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INTRODUCTION

Nearly all available information about small wild mammals has been obtained by indirect methods. The disadvantage of these methods is that they are likely to modify the behaviour of the animals, and it is usually impossible to assess the errors introduced. Trapping is frequently used in studies on movements but probably affects normal behaviour. A method which is believed to have little effect upon the animals' behaviour has been developed for the study of movements in field voles (*Microtus agrestis* L.). It consists of labelling the animals with radioactive material and tracking them with a Geiger-Müller counter unit. This method was used by Brian (1947) in a study of the movements of click beetles (*Agriotes*). The apparatus used here, however, differs from Brian's as it employs a low-voltage G-M tube and is independent of the mains power supply. The purpose of this paper is to describe the apparatus and some of the information which has been obtained with it in the field.

The work was carried out during 1949-51 in the University estate at Wytham, Berkshire. Voles labelled with radioactive material formed part of the two populations whose changes in numbers were simultaneously being studied by the marking-recapture method.

THE GEIGER-MÜLLER COUNTER UNIT

The counter unit employs a type G 10 H halogen-quenched G-M tube developed by 20th Century Electronics, Ltd., London, in collaboration with the Atomic Energy Research Establishment at Harwell. This tube has a plateau in the region of 300-350 volts so that it can be operated from a small dry battery. The background count is about 80/minute (shielded). A simple two-stage amplifier drives a pair of headphones (Fig. 1). The whole apparatus (Figs. 2, 3), with the G-M tube mounted on an extensible 5-ft. arm, is portable and weighs 5½ lbs. (2.5 kg.). It has proved reliable and robust in field use under exacting conditions.

Cobalt 60 was chosen as the source of γ-radiation on account of its long half-life (5.3 yrs.) and high-energy radiation (1.33 and 1.17 MeV). It is used in this work in the form of wire of 1 mm. diameter with a specific activity of 21 mc/g. The radioactive ring consists of a brass tube, open at both ends, with its wall soldered to a monel metal ring. This tube is 2.8 mm. in length with an ex-

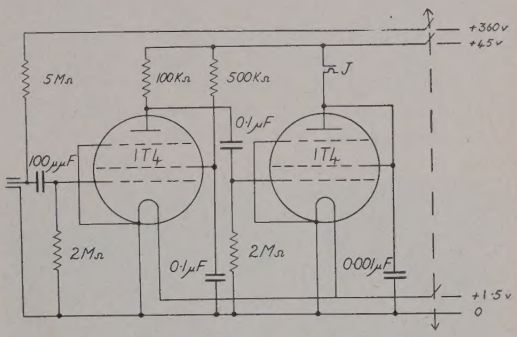


FIG. 1. Circuit diagram of the Geiger-Müller counter unit.

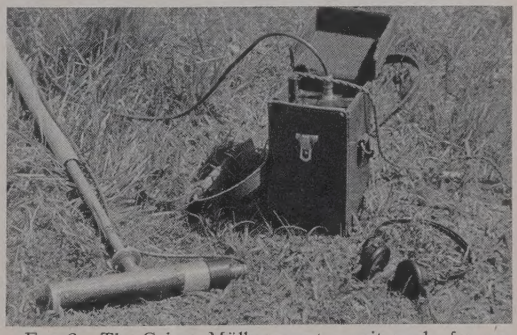


FIG. 2. The Geiger-Müller counter unit ready for use.

FIG. 3. The Geiger-Müller counter unit in use.

ternal diameter of 2.2 mm. and an internal diameter of 1.59 mm., and it encloses 5-10 mg. Cobalt 60 (100-200μc specific activity), held in the tube with plaster of Paris.

The radioative ring is a modification of the type used for small mammals in the Bureau of Animal Population (Chitty 1937). It is made from a monel metal strip 9 mm. x 3 mm. x 0.25 mm., which is bent into the form of a U and weighs 220 mg. Nestling young are ringed with a small U-shaped ring made from a monel metal strip 7 mm. x 2mm. x 0.25 mm. weighing 130 mg. The ring is fitted to the leg of the vole immediately above the ankle and is closed with pliers (Fig. 4).

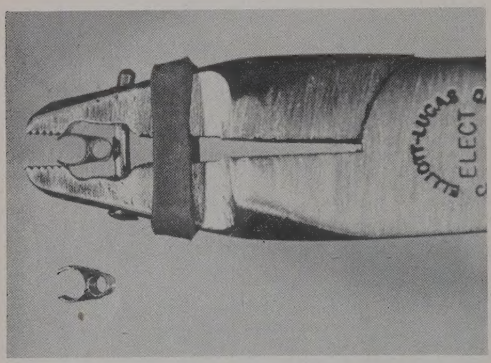


FIG. 4. Leg-ring for nestling voles, showing brass tube for Cobalt 60 and modified ringing pliers.

It is not known what effect this procedure has upon the health of the animals, but so far there is no indication that it disturbs pregnancy or causes other bodily changes. The animals do not carry radioactive rings longer than three months, and usually for a much shorter period. The β rays, which are more likely to be harmful than the γ rays, are shielded from the voles by the wall of the brass tube. Although no obvious physiological changes have been observed the possibility that the genetic constitution of these individuals and of their descendants has been affected should not be overlooked.

TECHNIQUE

During the location of a vole the G-M probe is held above the grass and moved in broad arcs in order to cover the ground in concentric circles about the point at which the animal was released. The distance from which voles can be detected depends upon the size of the γ-ray source and upon whether the animals are above or below the soil surface. Since they are rarely found on the study areas at a greater depth than 3" and are usually above the ground, and since the source normally used is 100μc specific activity, they are generally detected at 2-4' from the end of the probe (*i.e.*, 8-10' from the observer). For exact location the probe must be held directly above the tussocks. It may take a considerable time to find each animal on the first few occasions after its release but on subsequent occasions when its range is known location generally takes only a few minutes.

It is believed that the recordings of voles made at half-hourly and hourly intervals during this study had little effect upon their normal movements. It was usually possible to determine whether or not a vole was moving from the first moment it was detected, when it was 8-10' from the observer, and it is unlikely that location from this distance could have disturbed the animal. When a closer approach was made there was generally no change in the animal's movements, and if it was not moving when it was first located, it seldom started to move even when the cover directly above it was disturbed.

One of the principal difficulties encountered in this work was the continual disappearance of voles ringed with radioactive rings. Out of the 52 which were carrying Cobalt 60 rings and were studied between March and September 1951, no less than 29 were known to have disappeared from the areas. There was no evidence of emigration of voles at any time during the two years, and the woods surrounding the areas of grassland probably form complete barriers to movement. Another 7 animals disappeared leaving their rings on the study areas. It is extremely unlikely that these rings slipped off the legs, and in one case the leg was still inside the ring; the other hind leg, bearing an ordinary numbered leg-ring, was lying beside it. It is believed that predation was responsible for the disappearance of these animals.

The chief disadvantage of this technique is that it is difficult to distinguish between individuals, especially when there are a large number with radioactive rings in a small area. Rings were therefore generally attached to voles with adjacent rather than overlapping ranges. It proved possible, however, to distinguish between a few animals by making fairly large variations (*i.e.*, of the order of 100μc) in the size of the Cobalt 60 source.

ANALYSIS OF RESULTS

The problems encountered during the analysis of recordings made with the G-M counter are similar to those encountered during the analysis

of trapping records, except that they are concerned less with the validity of the data than with the interpretation. All current methods of analyzing trapping data involve the assumption—for which there is little evidence—that the animals do not travel to any important degree beyond the points at which they are captured (Hayne 1949). The use of the G-M counter ensures that movements are unrestricted, and consequently it enables the animals to be recorded at the boundaries of their ranges. Furthermore, since there is no risk of the animals' behaviour being modified through confinement, a large number of observations can be made in a short period.

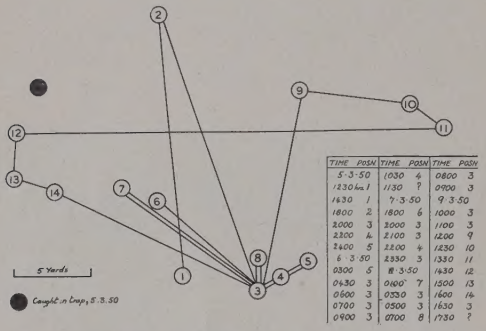
Throughout this paper the term "range" is used instead of "home range" (Burt 1943), and is defined as "that area traversed by the animal in its normal activities of food-gathering, mating, and caring for young." This definition is almost identical with Burt's except that the phrase "about its established home" is omitted.

Seven hundred and nine recordings of 23 voles made with the G-M counter form the basis for the following analysis. Two females and one male were recorded a total of 83 times at intervals of 1-1½ hrs. in 1950, and in 1951, 9 females were recorded 339 times in April at half-hourly intervals and 11 females were recorded 287 times between May and September at intervals of 24-48 hrs. (Table I). For each animal, the distance in yards between the two furthest points of location gave a measure of the length of the range (column 5). A measure of the breadth was given by the distance in yards between the two furthest points at right angles to this first measurement though not necessarily about its mid-point (column 6). As there were no significant differences between the three groups of data mean values were calculated for the 23 animals. The length of the ranges (29.04 yd.) was almost twice their maximum width (16.87 yd.). Estimates of area were made by joining the outside points of location of each animal, and from them a mean value of 235.17 sq. yd. or 0.048 acres was obtained (column 7). Areas calculated from the product of columns 5 and 6 exceed those shown in column 7 and are undoubtedly too large. It should be noted that the direct conversion of linear measurements into areas nearly always overestimates the sizes of the ranges, and indeed, for most animals the area ob-

TABLE I. *Measurements of the ranges of 23 voles which were studied with the G-M counter unit.*

1.	2.	3.	4.	5.	6.	7.
				Size of range		
Vole No.	Period studied	Number recordings	Reproductive condition	Length (yd.)	Breadth (yd.)	Area encl. by outside points of location (sq. yd.)
1950						
175m	Feb. 23-Mar. 6	17	Fecund	35	18	200
43 f	Mar. 4-19	33	Anoestrus	27	20	263
186 "	"	33	"	35	10	143
1951						
1 "	Apr. 3-13	43	"	29	13	200
2 "	"	45	"	26	16	175
5 "	"	36	"	23	16	250
6 "	"	34	"	33	22	360
7 "	"	48	"	22	15	148
265 "	"	50	"	29	25	376
RC2"	"	28	"	33	18	300
RC3"	"	27	"	28	10	208
RC4"	"	28	"	30	10	207
1951						
14 "	May 8-July 6	18	Preg. & Lact	30	20	175
YG1"	May 20-July 6	18	Immature	20	13	198
19 "	May 26-July 18	18	Preg. & Lact	32	15	180
24 "	June 22-Aug. 15	27	"	35	18	428
29 "	July 8-Sept. 3	28	"	35	15	126
32 "	July 31-Sept. 21	17	"	25	14	165
30 "	July 26-Sept. 24	40	"	23	17	177
31 "	July 31-Sept. 21	26	"	33	27	350
33 "	Aug. 2-Sept. 24	33	"	30	18	207
34 "	"	30	"	35	28	475
35 "	July 31-Sept. 22	32	"	20	10	98
			Mean	29.04	16.87	235.17
			S. E. ±	1.66	1.31	18.62

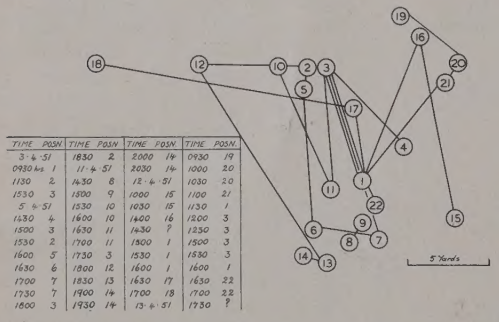
tained by multiplying length and breadth is more than twice the area obtained by joining the outside points of location. The rectangular range of No. 43 (Fig. 5), however, provides an exception, for the area is the same whether calculated directly from the linear measurements or obtained by joining the outside points of location. Except for this female, a better estimate of area is obtained if the length and breadth are regarded as the *diagonals* of a parallelogram.



TIME	POSN	TIME	POSN	TIME	POSN
5·3·50	1	1030	4	0800	3
1230 hrs	1	1130	?	0900	3
1630	1	7·3·50		9·3·50	
1800	2	1800	6	1000	3
2000	3	2000	3	1100	3
2300	4	2100	3	1200	9
2400	5	2200	4	1230	10
6·3·50		2330	3	1330	11
0300	5	11·3·50		1430	12
0430	3	0400	7	1500	13
0600	3	0530	3	1600	14
0700	3	0500	3	1630	3
0900	3	0700	8	1730	?

FIG. 5. Positions in which female No. 43 was located between March 5-9, 1950.

Even when 30-40 recordings have been made problems may still be introduced by the configuration of an animal's range. Thus in the crescent-shaped range shown in Figure 6, it is not known whether the area between the horns was used.

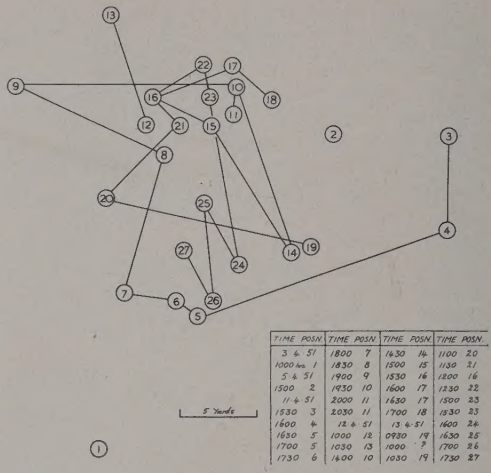


TIME	POSN	TIME	POSN	TIME	POSN	TIME	POSN
3·4·51		1830	2	2000	14	0930	19
0930 hrs	1	11·4·51		2030	14	1000	20
1130	2	1430	8	12·4·51		1030	20
1530	3	1500	9	1000	15	1100	21
5·4·51		1530	10	1030	15	1130	1
1630	4	1600	10	1400	16	1200	3
1500	3	1630	11	1430	?	1230	3
1530	2	1700	11	1500	1	1500	3
1600	5	1730	3	1530	1	1530	3
1630	6	1800	12	1600	1	1600	1
1700	7	1830	13	1630	17	1630	22
1730	7	1900	14	1700	18	1700	22
1800	3	1930	14	13·4·51		1730	?

FIG. 6. Positions in which female No. 2 was located between April 3-13, 1951.

In Figure 7, the outlying points introduce a difficulty: their inclusion is essential for consistency yet it adds considerably to the resultant area. A solution may be found for some of these problems when the run system becomes the basis for the study of ranges.

It is considered that most of the voles were recorded enough times for the limits of their ranges to have been revealed. The average number of recordings made and days which elapsed



TIME	POSN	TIME	POSN	TIME	POSN	TIME	POSN
3·4·51		1800	7	1430	14	1100	20
1000 hrs	1	1830	8	1500	15	1130	21
5·4·51		1900	9	1530	16	1200	16
1500	2	1930	10	1600	17	1230	22
11·4·51		2000	11	1630	17	1500	23
1530	3	2030	11	1700	18	1530	23
1600	4	12·4·51		13·4·51		1600	24
1630	5	1000	12	0930	19	1630	25
1700	5	1030	13	1000	?	1700	26
1730	6	1400	10	1030	19	1730	27

FIG. 7. Positions in which female No. 6 was located between April 3-13, 1951.

before the distance between the two furthest points of location reached a maximum was calculated for the two groups of data for 1951 (Table II). Group A comprises the 11 females which were recorded 287 times (an average of 26 times each) between May and September, while the data in group B refer to the 9 females which were recorded an average of 38 times each between April 3 and 13. The fact that 10 recordings/vole were made in group A and 19 in group B (column 3 minus column 1, last entry) without any increase in the distance between the two furthest points of location suggests that the limits of the range length had been reached. Although the area enclosed by the outer points of location still continued to increase with an increasing number of recordings per vole (column 2), it is probable that its limits were also eventually reached, as in each group several recordings were made without any further increase in area (column 3 minus column 2). Trapping records support this view, for as will be seen later, most of the voles were captured within the areas in which they were located with the G-M counter.

It has already been shown that the ranges of the two groups of voles were of approximately the same size. Since in both groups almost the same number of recordings are needed to obtain different percentages of the distance between the two furthest points of location (compare upper rows of column 1 in Table II), it is clear that the number of recordings is more important than their distribution in time when the limits of the range are being determined in a species such as *Microtus* which moves over a restricted area.

TABLE II. *The average number of recordings made before maximum values were obtained for the length and area of the ranges.*

	1. Minimum recordings needed to obtain different % of length of range						2. Minimum recordings for area of range	3. Total recordings
	25%	50%	75%	90%	95%	100%		
(A) 11 females studied between May 8 and Sept. 24, 1951.								
Recordings/vole....	3.6	4.5	7.5	14.3	16.1	16.4	19.4	26.1
Days/vole.....	7.7	8.9	15.6	32.0	36.6	37.2	41.5	56.7
(B) 9 females studied between April 3 and 13, 1951.								
Recordings/vole....	4.4	6.7	8.0	17.0	17.0	19.0	28.3	37.7
Days/vole.....	1.6	3.1	4.0	5.6	5.6	6.3	8.4	9.0

Routine trapping was carried out at intervals of 2-4 weeks during 1950 and 1951. After pre-baiting, the live-traps were placed 7½ yd. apart so that several were available normally within each animal's range. Twelve of the 23 voles listed in Table I were trapped during the periods in which they were being studied with the G.M. counter, and 8 of them were caught only within the areas enclosed by the outside points of location. Twenty captures were made altogether. There is no evidence from these records that the areas enclosed by the points of location underestimated the sizes of the ranges.

The remaining 4 animals, however, were trapped outside the areas in which they were located (Table III). In the case of No. 34, the distance involved was small, and the area in which this female was located (Table I, column 7), was larger than that of any other animal; although 31 recordings were made, they were apparently insufficient to reveal the boundaries of the range.

TABLE III. *Records of voles trapped outside the areas in which they were located with the G-M counter unit.*

1. Vole Number	2. Period studied	3. Distance trapped outside the area enclosed by the outer points of location (yd.) before study period	4. during study period	5. after study period
	1950			
175....	Feb. 23-Mar. 6....	17, 17, 17, 25	0, 17	0, 20, 40, 40, 40
	1951			
14.....	May 8-July 6....	3, 5, 5, 7, 7, 15	0, 20	
30.....	July 26-Sept. 24....	10	0, 2, 10, 60	
34.....	Aug. 2-Sept. 24....	5, 7	0, 7	3, 3

The distances involved were also relatively small on 2 out of the 3 occasions on which No. 30 was caught outside the area in which it was located. The 60-yd. movement is discussed in detail elsewhere[1]. For the present purpose, it is regarded as the type of movement which Burt (1943) terms an occasional sally from the home range. In neither of these cases is there evidence of a marked discrepancy between the positions in which the voles were located and the positions in which they were trapped.

Nos. 14 and 175, on the other hand, were trapped at considerable distances outside the areas enclosed by the points of location. They were recorded less than the average number of times and their ranges were less than the average size (Table I). It is clear that the data obtained with the G-M counter were insufficient to reveal the boundaries of these ranges.

Several of the voles bearing Cobalt 60 rings were located with the counter during the routine trapping. On one occasion an animal was known to have passed within a foot of a trap, and to have remained half an hour in its vicinity without entering. Another animal, which was ringed as a nestling, was never trapped although the traps were often placed in the actual positions in which it had been located. These facts suggested that some of the voles might have been exhibiting a more persistent trap-shyness than that already described for *Microtus* (Chitty & Kempson 1949). In order to see whether certain individuals were missing capture more frequently than would be expected under a hypothesis of a random distribution, Mr. P. H. Leslie kindly suggested the following method of analysis.

Since the day on which each of the animals bearing Cobalt 60 rings disappeared from the areas was known, the numbers alive in the different trapping periods could be calculated. These are shown in Table IV, column 2, with the numbers marked and released in each period in heavy type. The numbers trapped are given in column 4. The mean probability of being trapped on any one occasion = 25/44, or $\bar{p} = 0.568$. The mean probability of not being trapped, or $\bar{q}$, therefore, is 0.432. Twenty-six animals were exposed to risk in at least one period following the one in which they were marked with a Cobalt 60 ring and released. An examination of their individual records showed that 11 were exposed to risk in one subsequent period, 12 in two periods, and 3 in three periods. Of the voles which were at risk in one period only, 7 were caught and 4 missed, while the expected numbers are 11 x 0.568 = 6.25, and 11 x 0.432 = 4.75 respectively.

The following possibilities are available to the 12 voles which were exposed to risk in two periods, namely, being caught twice (XX), being missed twice (OO), or being caught once and missed once (XO or OX). The numbers ex-

[1] Godfrey, G. K. D. Phil. thesis, on file at the Bodleian Library and the Bureau of Animal Population, Oxford.

TABLE IV. *Voles bearing cobalt 60 rings at risk during the different trapping periods in 1951.*

1. Trapping period (*one area only)	2. Voles exposed to risk								3. Total at risk	4. Total trapped
Mar. 18-21	**13**									
Apr. 16-19	9	**1**							9	4
May 2-3*	4	1	**11**						5	5
May 21-24	3		5	**4**					8	5
June 11-16			1	2	**9**				3	2
July 4-5*			1	2		**1**			3	0
July 20-28				1	2	1	**7**		4	1
Aug. 27-Sept. 1					1	1	5	**6**	7	5
Sept. 24-29							4	1	5	3
									44	25

pected in the different classes under the hypothesis of a purely random distribution of recaptures are given by the expansion of the binomial distribution $12\,(0.568 + 0.432)^2$, and these are shown below, together with the numbers observed in each class.

	XX	XO + OX	OO	Total
Observed	3	7	2	12
Expected	3.87	5.89	2.24	12

Only 3 voles were exposed to risk in three periods. Of these, 2 were caught twice and missed once, while one missed twice and was caught once. The numbers expected in the different classes are shown below.

	XXX	XXO	XOO	OOO	Total
Observed	0	2	1	0	3
Expected	0.55	1.26	0.95	0.24	3

There is clearly no evidence from these data that there was greater heterogeneity than would be expected in the trap response of individual voles.

ACKNOWLEDGMENTS

This work was carried out at the Bureau of Animal Population, Oxford, between 1949 and 1951. Acknowledgment is made to the Director, Mr. C. Elton, for the provision of the Bureau's facilities, to Mr. P. H. Leslie and Dr. Dennis Chitty for advice and criticism, and to Mr. Denys Kempson for assistance and forbearance in the workship. Acknowledgment is also due to members of the Clarendon Laboratory, particularly to Mr. K. Mayne for building and servicing the Geiger-Müller counter unit, and to Dr. D. F. Shaw for arranging for the routine blood counts and examination of films. Photographs (Figs. 2-4) are by Denys Kempson.

SUMMARY

This paper describes a portable Geiger-Müller counter unit developed for tracing the movements of field voles (*Microtus agrestis* L.). Cobalt 60 is used as the source of γ-radiation. Brass tubes containing approximately 100μc (5-10 mg.) are soldered to monel metal rings which are fitted to the legs of the voles with modified pliers. Voles bearing these rings can be detected at 8-10′ from the observer, though in order to determine their positions accurately it is necessary to approach to within 2-4′.

During this study, 709 recordings were made of 23 voles. The average distance between the two furthest points of location of the 23 animals was 29.04 yds. while the area obtained by joining the outside points of location was 235.17 sq. yds. or 0.05 acres. The average length of the ranges showed no increase after 19 recordings had been made, though the average area continued to increase. When no further increase in area occurred it was assumed that the limits of the ranges in all directions had been determined. Ten voles were trapped only within, or at short distances outside the areas in which they were located, suggesting that for these animals the conclusion was a justifiable one. Two voles, however, were trapped 17 and 20 yd. respectively outside the areas in which they were located showing that insufficient recordings had been made to reveal the boundaries of their ranges.

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THE REGENERATION OF *PRUNUS SEROTINA* IN NORTHWESTERN PENNSYLVANIA FOLLOWING CUTTING

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Black cherry, *Prunus serotina* Ehrh.,[1] is a very important species in the forests of the High Plateaus Region of northwestern Pennyslvania as described by Hough and Forbes (1943). In this area, it attains large size, excellent form, and is a major component of the hardwood forest. Its importance is indicated by a report of the Forest Survey (1948) for four counties lying in the heart of this region. In these four counties, black cherry leads all other species with 20.9 per cent of the total net board-foot volume, and 18.9 per cent of the total net cord wood volume of all species on all commercial forest land. The rapid growth and value of this species combined with its abundance make *Prunus serotina* an extremely desirable species to manage in northwestern Pennsylvania.

The principal problem with which foresters have been confronted up to this time has been to find methods of regeneration which will produce stands of reproduction with a high percentage of vigorous, high-quality individuals. Accordingly, a study was undertaken to determine the relative success or failure of *Prunus serotina* regeneration under the environmental conditions which prevailed following various methods of cutting.

The principal objective of the study was to determine the success of reproduction in relation to the density of the remaining stand (called residual stand density) and the form of cutting used. The density of the remaining stand was measured in terms of square feet of basal area per acre of all trees having a diameter of 0.6 inches or above at 4.5 feet above the ground (called the d.b.h. point). The residual stand here means that portion of a forest stand left standing following a cutting. This measure was used since it appeared to be the most applicable and reliable method of comparing the conditions in the series of stands studied. Light intensity, *per se,* was not thought to be a desirable measure in this study since it would have little meaning in some of the stands studied. An acre completely devoid of trees following a clear cutting and another acre with possibly three residual trees could show the same light intensity on almost their entire areas, although conditions for reproduction would appear to differ, for example, as to seed source.

In studying the success or failure of reproduction, it is necessary to recognize the form of cutting in addition to the density of the remaining stand. This is necessary since the same residual stand density might result from two forms of cutting; for example clear cutting on a narrow strip or clear cutting on a large area.

To appraise the success of reproduction, it was necessary, therefore, to study the reproduction under undisturbed conditions and on different forest areas resulting from various methods of cutting.

Sampling was done on as great a variety of areas, representing existing stand conditions, as could be located. The sampled areas were grouped into the following thirteen distinct classes, representative of typical conditions in the northern hardwood forests of northwestern Pennsylvania.

1. *Clearcut strips*—The two areas in this condition class consisted of narrow strips 66 by 660 feet on which the entire 30-year-old second-growth stand had been removed 26 years earlier.
2. *Group cutting to a 5-inch diameter limit*—Eleven years earlier all trees had been removed down to a 5-inch d.b.h. on a .5-acre plot from a 45-year-old second-growth stand.
3. *Group cutting to an 8-inch diameter limit*—Eleven years earlier all trees had been removed down to an 8-inch d.b.h. on a .7-acre plot from a 45-year-old second-growth stand.
4. *Group cutting to an 11-inch diameter limit*—Eleven years earlier all trees had been removed down to an 11-inch d.b.h. on a 1-acre plot from a 45-year-old second-growth stand.
5. *Large-scale clearcut*—This class consisted of seven large tracts approximately 200 acres in size on which the 40- to 50-year-old second-growth had been clearcut from 4 to 20 years prior to examination.
6. *Clearcut with seed trees*—A second-growth northern hardwood stand had been cut 25 years earlier leaving 15 *Prunus serotina* seed trees per acre.
7. *Clearcut and burned*—Two tracts of about 200 acres of second-growth northern hard-

[1] Nomenclature of tree species in this paper is that of Harlow and Harrar (1950).

woods had been cut 24 years previously and were then burned by a forest fire.

8. *Thinned second-growth*—Seven stands of 50-year-old second-growth had been thinned during the 15 years prior to examination. These partial cuttings consisted of the removal of about 40 per cent of the cubic volume in the form of the inferior-quality, slow-growing trees.
9. *Continuously thinned and grazed*—A farm woodlot of about 20 acres had been continuously subjected to thinnings for the past 25 years removing a few trees annually but not disrupting the continuity of the crown canopy to any extent. The area was also subjected to intermittent grazing by cattle. At the time of examination, the stand was 56 years old.
10. *Continuously thinned, not grazed*—This was another portion of the above-mentioned woodlot cut in a similar manner but not grazed.
11. *Selectively-cut old-growth*—This stand consisted principally of old-growth trees plus some second-growth that had come in following light cuttings in the 1890's. The stand was again lightly cut in 1947, removing some of the larger trees down to a diameter limit of 16 inches on an area of 173 acres.
12. *Uncut second-growth*—This stand originated following a large-scale clear-cutting 40 to 50 years ago. There had been no cutting since the stand originated.
13. *Old growth virgin*—This stand consisted of a tract of old-growth timber which originated following a severe windthrow 127 years earlier. No cutting of any type had ocurred.

Methods of Study

The reproduction in the stands representative of these thirteen stand condition classes was sampled by means of a two-part survey consisting of an extensive and an intensive survey.

The extensive survey consisted of establishing 4-milacre quadrats at intervals of 2 chains (132 feet) along a compass line to determine the frequency of *Prunus serotina* and its importance in the reproduction. All topographic positions, elevations, aspects, slope steepnesses, and reproduction ages classes that occurred were sampled. Soil types were not studied since the soils upon which the sample areas were taken were homogeneous and were not thought to exert any controlling influence. Topographic position refers to the general location such as plateau top, upper slope, middle slope, lower slope, or valley bottom. The other terms are self-explanatory.

An adaptation of the "stocked quadrat" method of Wellner (1940) was used. If any *Prunus serotina* reproduction one year or older occurred on a quadrat, it was called "stocked." The tallest individual of any tree species in the reproduction on the quadrat was called the "principal." This principal individual is the tree in the reproduction on the quadrat that has the greatest likelihood of reaching maturity. If it is a species considered of commercial importance, it probably will be the tree on the quadrat that will form a part of the harvest. Although the limitations of this concept were realized, this measure does serve as a means of roughly forecasting the future stand. The species, origin, vigor, and quality class of the principal on each plot was recorded. Three origin classes were recognized: seedling, seedling-sprout, and stump-sprout or root-sucker. Each principal was classified as to its most probable origin. Seedlings were trees originating from seed; seedling-sprouts arose from low stumps less than 3 inches in diameter; and stump-sprouts were trees originating from larger stumps or root suckers. Vigor class depended upon the color and density of the foliage, crown size, position with relation to competitors, and space available for growth. The vigor classes were:

I—Dense foliage of good color. Large crown completely free to grow. Fast height or diameter growth.

II—Foliage not very dense. Medium-sized crown, slightly crowded or overtopped. Moderate height or diameter growth.

III—Scanty foliage of poor color, serious defects or injuries present. Small crown completely overtopped or crowded. Slow height or diameter growth.

Quality classes were based on the form of the individual. The quality classes were:

I—Good form, straight main stem, crown well-formed, branches small.

II—Fair form. Main stem with some deformities, crown not well-formed, large branches.

III—Poor form. Main stem with many deformities or no definite central stem present. Crown poorly formed, large branches.

The amount of current regeneration of *Prunus serotina* on each quadrat was determined. Current regeneration refers to those individuals which germinated during the year of examination. Four density classes were used:

Dense—51 or more stems per quadrat
Moderate—11 to 50 stems per quadrat
Sparse—1 to 10 stems per quadrat
None—0 stems per quadrat

The second part of the study, the intensive sur-

vey, consisted of establishing .1-acre blocks in the same areas extensively surveyed. A complete tally was then made of all the tree reproduction one year or older on five 4-milacre quadrats randomly selected from the 25 comprising the total block. The density of the residual or older stand, when present, was recorded for a .2-acre circular plot containing the .1-acre block. The primary purpose of the intensive phase of the survey was to obtain information on the density of the residual or older stand and to specifically describe the total tree reproduction population. On the intensively examined quadrats, every individual in the reproduction one year or older was recorded by species. The height or diameter growth rate of the principal individual on each quadrat was also recorded.

Results

The average residual stand densities for the various stand condition classes are shown in Table I. An attempt was made to correlate these residual stand densities with the relative reproductive success or failure of *Prunus serotina*. Statistical analyses, using the Chi-square test and the F test with an analysis of variance were also carried out to assess the influence of the site factors recognized on *Prunus serotina* reproduction. Aspect was the only factor that seemed to be of any importance. Somewhat poorer reproduction in amount and size was found on south and west-facing aspects when compared to north and east ones.

Frequency of Prunus serotina in extensive survey

High frequency percentages for *Prunus serotina* reproduction were found in all the stand conditions sampled by the extensive survey as shown in Table I. Frequency indicates the percentage of the quadrats examined upon which the species occurred (the "stocked" quadrats). The group cutting to an 8-inch diameter limit had 100 per cent frequency, followed closely by the other two group cutting classes and the strip cutting. Only two stand condition classes had frequencies below 60 per cent.

Statistical analyses to determine whether or not significant differences existed in the frequencies of *Prunus serotina* in the different stand condition classes were carried out. The differences between all but two could have been due to chance. The variation between the high frequencies for the 8-inch-d.b.h. limit cutting and the low ones for the untreated second growth were statistically significant.

It is clear that the occurrence of *Prunus serotina* in the residual or older stand, or in the immediate vicinity, is of little moment in the frequency of established *Prunus serotina* reproduction. Reference to the basal area figures in Table I supports this conclusion. Large-scale clearcuttings had a 70 per cent frequency although the closest seedbearing trees were sometimes a half-mile away. The seed-tree cutting had *Prunus serotina* trees scattered over the immediate area yet the frequency was less than for large-scale clearcuttings.

The density of the residual or older stand had little effect on the frequency percentages. A large number of the plots examined in every stand condition class had some *Prunus serotina* reproduc-

Table I. *Residual or older stand densities and frequency of Prunus serotina reproduction in 13 stand condition classes*

Stand condition class	Age of stand when cut (years)	Present age of residual stand (years)	Time since cutting (years)	Basis quadrats sampled (number)	Average stand density per acre (Square feet of basal area)				Frequency of *Prunus serotina* reproduction (per cent)
					After cutting		In 1950		
					All species	*Prunus serotina*	All species	*Prunus serotina*	
Clearcut strips	30	*	23-26	28	0.0	0.0	0.0	0.0	79
Group cutting to a 5 inch diameter limit	45	54	11	18	3.0	0.0	43.6	0.0	83
Group cutting to an 8 inch diameter limit	45	54	11	18	28.6	4.6	82.4	4.9	100
Group cutting to an 11 inch diameter limit	45	54	11	18	54.9	19.7	99.4	18.5	83
Large-scale clearcut	40-50	*	4-23	183	0.0	0.0	0.0	0.0	70
Clearcut with seed trees	58	83	25	10	6.6	6.6	23.5	16.8	60
Clearcut and burned	40-50	*	24	20	0.0	0.0	0.0	0.0	55
Thinned second growth	35-42	40-55	5-13	95	81.3	21.1	100.6	27.9	76
Continuously thinned and grazed	†	55	†	10	‡	‡	102.6	46.1	80
Continuously thinned, not grazed	†	65	†	10	‡	‡	113.6	40.5	90
Selectively-cut old growth	all-aged	all-aged	‡	30	‡	‡	140.8	112.1	80
Uncut second growth	..	53	..	10	..	..	137.9	60.3	40
Old-growth virgin, uncut	..	123	..	10	..	..	178.9	118.8	70

*No residual stand. †Continuous thinning did not allow dating. ‡No data available.

TABLE II. *Percentages of quadrats examined in extensive survey having various species as the principal individuals*

Stand condition class	Principal individuals										
	Prunus serotina	*Acer saccharum*	*Fagus grandifolia*	*Prunus pennsylvanica*	*Acer rubrum*	*Ostrya virginiana*	*Carpinus caroliniana*	*Acer pennsylvanicum*	*Others**	*None*	Total
Clearcut strips	68	18	..	4	7	3	..	..	..	..	100
Group cutting to a 5 inch diameter limit	50	..	50	..	..	..	..	..	..	..	100
Group cutting to an 8 inch diameter limit	44	..	56	..	..	..	..	..	..	..	100
Group cutting to an 11 inch diameter limit	16	..	67	..	..	..	..	17	..	..	100
Large-scale clearcut	27	21	7	5	13	18	7	3	8	1	100
Clearcut with seed trees	10	10	..	..	10	30	20	..	10	10	100
Clearcut and burned	40	10	..	5	5	..	..	..	20	20	100
Thinned second growth	6	25	33	1	..	5	1	12	11	11	100
Continuously thinned and grazed	50†	10	..	..	..	..	..	..	20	20	100
Continuously thinned, not grazed	..	100	..	..	..	..	..	..	..	..	100
Selectively-cut old growth	..	47	30	..	3	3	..	6	1	10	100
Old-growth virgin, uncut	..	40	60	..	..	..	..	..	..	..	100

*Others include; *Populus tremuloides, Tsuga canadensis, Betula lenta, Betula lutea, Frazinus americana, Amelanchier canadensis,* and *Acer spicatum.*
†All below 1 foot in height. The only tree species present on these quadrats.

tion over a year old although the residual or older stand densities varied widely.

The frequencies indicate that *Prunus serotina* is well able to become initially established in the reproduction of all stand conditions studied. That this initial establishment does not assure the species having an important role in the ultimate stand of reproduction will be demonstrated by the percentages of the principal individuals. It appears that the germination and establishment of *Prunus serotina* reproduction is not critical. The problem is to ascertain the environmental conditions under which this early reproduction will successfully develop and then devise techniques that will produce these conditions in managed stands.

Principal individuals in extensive survey

The percentages of *Prunus serotina* and associated species constituting the principal individuals on the quadrats examined are shown in Table II. These pecentages show the relative number of quadrats upon which the various species were classed as the principal individuals. The combination of the areal extent of cutting and the form and density of the residual or older stand seem to be the key factors in the importance of *Prunus serotina* reproduction. The three treatments that produced the greater percentage of *Prunus serotina* as the principal individuals were complete removal of the overwood in a narrow 1-chain-wide strip or removal of all trees down to a 5- or 8-inch d.b.h. limit on .5- to 1-acre patches. Large-scale clearcuttings also showed high percentages of *Prunus serotina* as the principal individuals.

An analysis of variance to see if the different percentages were significant was carried out. This analysis disclosed that the clearcut strips and the 5- and 8-inch d.b.h. limit cuttings had significantly more *Prunus serotina* reproduction classed as the principal individuals than all the other condition classes but did not differ among themselves.

The stand conditions with the highest percentages had either a sparse residual stand or complete exposure on a limited area. The low-diameter-limit cuttings and narrow clearcut strips produced similar environmental conditions. The narrow strips did not expose the forest floor completely to the climatic vicissitudes because of the moderating effect of the enclosing stand. The low-diameter-limit cutttings had a light cover of small trees over the entire area producing a similar effect.

Complete removal of the forest on wide areas as in the large-scale clear-cuttings, or denser residual stands than that present in the 5- and 8-inch-d.b.h. limit cuttings, resulted in far less *Prunus serotina* classed as the principal individuals.

These findings indicate that *Prunus serotina* needs some protective cover or influence in early youth to become successfully established and assure its initial development. This requirement is of primary importance in applying regeneration cuttings if *Prunus serotina* is to be favored. The regeneration cutting must be so executed that the site is not too densely shaded by the residual stand.

To cast further light on the character of the reproduction, the principal individuals of *Prunus serotina* were classed as to origin, vigor, and quality. All of the principal individuals of *Prunus serotina* in every condition class except clearcut strips and large-scale clearcuttings were either of seedling-sprout or seedling origin. On the

clearcut strip and large-scale clearcuttings about 25 per cent of the principal individuals of *Prunus serotina* were of stump-sprout origin. In spite of the fact that statistical significance was not proven, the high percentages of sprout origin in the last two mentioned condition classes is worth heeding.

High percentages of *Prunus serotina,* designated as principal individuals, in vigor classes I and II were found in stand condition classes with low residual stand densities. Clearcut strips, group cutting to a 5-inch diameter limit, large-scale clearcuttings, and the seed-tree cutting all had 100 per cent in the I and II vigor classes. Stand condition classes with higher residual or older stand densities had proportionately fewer individuals in the good vigor classes and more in the poor class.

The highest percentages of the principal individuals of *Prunus serotina* in the I and II quality classes occurred on the clearcut strips. The other condition classes with low residual or older stand densities had somewhat less in the I and more in the II and III quality classes. Those condition classes with denser residual or older stands had all the principal individuals of *Prunus serotina* in the III quality class.

Current regeneration of Prunus serotina in extensive survey

As shown in Table III, current *Prunus serotina* regeneration was found in every condition class sampled. Densest regeneration was found in the old-growth, thinned second-growth, and group cutting to an 11-inch diameter limit. These stand condition classes had the densest residual or older stands. Condition classes with sparser residual or older stands had less current reproduction. A favorable stand of reproduction is likely to result if regeneration cuttings can be timed so that they occur at the age of the older stand when current regeneration is best.

Density of all species in intensive survey

Table IV shows the density of the reproduction of all species found on the intensively examined quadrats. *Prunus serotina* was found in every stand condition class and had the greatest density in 7 of the 12 condition classes examined and high densities in the other 5 classes. *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh. ranked next with a marked decrease in the densities of the numerous other species encountered. It is interesting to note that the greatest density of established *Prunus serotina* occurred in those condition classes having a residual or older stand present. This was partly attributable to the fact that the condition classes with no residual or older stands had older reproduction and thus normally fewer trees. The maximum density of established *Prunus serotina* reproduction was found in the selectively-cut old-growth stand 3 years after logging. Over 380 stems per 4-milacre quadrat, equivalent to 95,200 stems per acre, were observed. *Prunus serotina* here comprised almost all the tree reproduction but it was small and of low vigor and poor quality.

Growth rates of Prunus serotina in intensive survey

The principal individual on each of the intensively examined quadrats was also noted. The

TABLE III. *Density of current Prunus serotina regeneration in thirteen stand condition classes sampled*

Stand condition class	Time since cutting (years)	Residual or older stand basal area in 1950 (sq. ft.)		Basis quadrats sampled	% of quadrats sampled according to density				
		Total	*P. serotina*		Dense (51+ per plot)	Moderate (11 to 50 per plot)	Sparse (1 to 10 per plot)	None (0 per plot)	Total
Clearcut strips	23-26	0.0	0.0	28	18	4	50	28	100
Group cutting to a 5 inch diameter limit	11	43.6	0.0	18	..	..	33	67	100
Group cutting to an 8 inch diameter limit	11	82.4	4.9	18	11	17	33	39	100
Group cutting to an 11 inch diameter limit	11	99.4	18.5	18	39	22	28	11	100
Large-scale clearcut	4-23	0.0	0.0	183	1	1	11	87	100
Clearcut with seed trees	25	23.5	16.8	10	..	..	40	63	100
Clearcut and burned	24	0.0	0.0	20	5	..	55	40	100
Thinned second growth	5-13	100.6	27.9	95	27	17	26	30	100
Continuously thinned and grazed	*	102.6	46.1	10	40	20	40	..	100
Continuously thinned, not grazed	*	113.6	40.5	10	60	20	20	..	100
Selectively-cut old growth	3	140.8	112.1	30	20	20	23	37	100
Uncut second growth	..	137.9	60.3	10	..	30	..	70	100
Old-growth virgin, uncut	..	178.9	118.8	10	50	10	30	10	100

*Continuous thinning did not allow dating.

TABLE IV. *Density of all reproduction on intensively sampled areas* *

Stand condition class	1	2	3	4	5	6	7	8	9	10	11	12
Number of quadrats sampled	10	10	10	10	60	5	10	35	5	5	5	5
Species density (Aver. number of individuals per quadrat)												
Prunus serotina	1.3	33.3	89.9	17.6	4.3	1.2	6.4	17.6	61.6	5.8	380.8	26.0
Acer saccharum	4.5	...	.1	...	9.4	5.0	...	20.8	2.0	7.8	17.6	5.0
Fagus grandifolia	.1	13.7	1.7	3.3	4.0	.2	...	3.0	...	...	2.6	11.8
Ostrya virginiana	.2	...	...	...	2.5	3.4	...	.7	.2	3.2	.2	.6
Carpinus caroliniana	...	...	...	...	2.4	1.8	1.9	.03	...	...	...	...
Fraxinus americana	...	...	...	...	6.9	...	...	...	...	.8	1.2	...
Prunus pennsylvanica	...	.1	...	...	.9	.8	...	.4	...	...	...	...
Sorbus americana	...	...	...	...	.02	...	...	...	.2	...	...	...
Cornus alternifolia	...	...	...	...	.1	...	...	...	...	...	...	...
Acer rubrum	.7	5.0	.2	.8	1.2	1.4	1.2	.5	1.0	...	...	2.0
Amelanchier arborea	...	...	...	.3	.5	2.6	.2	.1	.2	...	...	...
Quercus borealis	...	...	...	...	.1	...	...	...	...	...	...	...
Ulmus americana	...	...	...	...	.1	...	...	...	...	...	...	...
Acer spicatum	...	...	...	...	...	...	...	...	...	...	.4	...
Betula lutea	...	17.3	1.2	.9	2.0	1.4	...	.03	...	...	5.6	...
Populus tremuloides	...	...	...	...	.7	...	2.6	...	...	...	...	...
Tsuga canadensis	...	.2	.2	.3	.1	...	...	.3	...	...	...	.2
Salix spp.	...	...	...	...	.02	...	...	...	...	...	...	...
Tilia americana	...	...	...	...	.02	...	...	...	...	...	...	...
Magnolia acuminata	...	...	...	...	.02	...	...	.03	...	...	...	...
Populus grandidentata	...	...	...	...	.1	...	...	...	...	...	...	...
Crataegus spp.	...	...	...	...	.03	...	...	...	...	...	...	...
Liriodendron tulipifera	...	...	...	...	.02	...	...	...	...	...	...	...
Betula lenta	...	.6	...	...	...	...	...	.4	.2	...	...	...
Acer pennsylvanicum	...	.7	.6	.2	.9	...	...	2.1	...	...	1.0	.8

*The numbers designate the following condition classes: 1. Clearcut strips; 2, Group cutting to 5″ limit; 3, Group cutting to 8″ limit; 4, Group cutting to 11″ limit; 5, Large-scale clearcut; 6, Clearcut with seed trees; 7, Clearcut and burned; 8, Thinned second growth; 9, Continuously thinned and grazed; 10, Continuously thinned, not grazed; 11, Selectively-cut old growth; 12, Uncut second growth. Old-growth virgin condition class not sampled intensively.

growth rates of all *Prunus serotina* here classed as the principal individuals were measured in terms of 5-year radial increment at d.b.h. for those stems large enough to be sampled with an increment borer. The average annual leader growth was used as a measure of growth for smaller individuals.

Table V shows that the growth rates for the large-scale clearcuttings and the strip clearcuttings were quite uniform. Clearcut and burned areas had a slower growth rate possibly attributable to the deterioration of the site following burning. No *Prunus serotina* classed as the principal individual was found in the intensively examined quadrats in the seed-tree cutting.

In the other stand condition classes where a residual or older stand was present, leader elongation was used because the reproduction was too small for increment borings. The fastest leader growth occurred in the group cutting to a 5-inch diameter limit where it was 3 times as rapid as in the 8-inch-diameter limit cutting and over 20 times faster than in the thinned second-growth.

TABLE V. *Growth rates of Prunus serotina classed as the principal individuals in various stand condition classes* *

Stand condition class	Time since cutting (yrs.)	Average 5-year radial increment			Average annual leader growth		
		S	Ss	Sp	S†	Ss†	Sp†
No residual or older stand							
Clearcut strips	23-26	.52″	.47″				
Large-scale clearcut	4-23	.55″	.60″	.95″			
Clearcut and burned	24	.31″	.24″				
Residual or older stand present							
Group cutting to a 5 inch diameter limit	11	...	...	...	1.40′		
Group cutting to an 8 inch diameter limit	11	...	...	...	.54′		
Thinned second growth	5-13	...	...	...	.07′		
Continuously thinned and grazed	....	...	...	...	.10′		

*Growth rates are only shown for those condition classes in which *Prunus serotina* was noted as the principal individual during the intensive survey. Where no entry is shown it indicates no representative was found.
†S is seedling, Ss is seedling sprout, Sp is stump sprout or root sucker.

SUMMARY

1. *Prunus serotina* is the most ubiquitous species found in the current and established reproduction of areas sampled in the northern hardwood type in northwestern Pennsylvania.

2. *Prunus serotina* seed is widely distributed and germination seems to take place without any difficulty in this region. Densest current regeneration was found beneath seed-bearing trees. However the proximity of seed source has little

influence on the density of the established reproduction. The frequency of established *Prunus serotina* on the different areas studied did not seem to be affected by the nearness of seed trees.

3. Seedlings survived and grew best under light residual stands or open areas and on sites relatively free from competition with dense grass or herbaceous vegetation.

4. *Prunus serotina* reproduction became established and survived up to approximately 10 years under thinned or uncut 40- to 55-year-old second-growth and in old-growth stands. Such seedlings grew very slowly and suffered high mortality unless released by removal of the older stand.

5. *Prunus serotina* never attained the position of principal individual following thinning of second-growth, selective cutting of old-growth or in uncut second- and old-growth stands. In general, if the residual or older stand density was more than 50 square feet of basal area per acre following cutting, little *Prunus serotina* reproduction reached the position of the principal individual.

6. *Prunus serotina* reproduction became established and developed successfully under the open conditions following clearcutting or on narrow strip cuttings. Best results were found on narrow clearcut strips where the reproduction was not subjected to the climatic extremes found on extensive clearcut areas. *Prunus serotina* formed a high percentage of the principal individuals in stands cut to a 5- or 8-inch diameter limit on small areas leaving from 3 to 30 square feet of basal area per acre. *Prunus serotina* had fewer representatives classed as the principal individuals in large-scale clearcuttings and high percentages were of sprout origin and poor quality.

7. *Prunus serotina* grew faster than its associates in the open or under a light residual stand. Under denser residual or older stands, the vigor of *Prunus serotina* reproduction diminished and was surpassed by that of the more shade-tolerant species.

8. *Prunus serotina* stump-sprouts grew faster than seedlings or seedling-sprouts but were generally of poorer quality because of bole deformities, large branches, weak basal attachment, and the likelihood of rot from the parent stump.

9. Stand condition classes with a residual or older stand had no *Prunus serotina* of stump-sprout origin classed as the principal individuals. In contrast, reproduction on areas without a residual stand had large numbers of stump-sprout origin.

10. *Prunus serotina* regeneration attained best form and quality when in association with a large number of adjacent reproduction stems of the same species. If grown in the open, as in large-scale clearcuttings, its scatered occurrence coupled with its rapid rate of growth caused it to attain a greater height than most of its associates of other species. The trees then tended to spread in a lateral direction developing many branches and tending to lose an excurrent form.

Based on the evidence available from this study, clearcutting in narrow strips or cutting to low diameter limits in small patches are promising methods of regenerating *Prunus serotina*. The reproduction on clearcut strips appears to have made far better development than that in the diameter limit cuttings. Under forest management practices, even better results could be obtained through the control of unwanted sprouts of *Prunus serotina* and associated species by stand improvement measures.

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VARIATIONS IN BEACH SEINE SAMPLES CAUSED BY NET LENGTH AND REPEATED HAULS[1]

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Beach seines of various designs have been the principal gear used in qualitative studies of the littoral fish of Puget Sound, Washington. Records of beach seine catches in the vicinity of Seattle that cover a thirty-year period are available at the School of Fisheries, University of Washington.

Past hauls probably give a rather complete representation of the littoral species of fish in the areas sampled, but are of less value for the elucidation of even the simplest quantitative ecological problems. For example, a description of the seasonal appearance of a species is valid only if the sampling effort was sufficient to produce representative and consistent samples of the area under study. More specifically, will one beach seine haul produce a representative sample of the population present, or are repeated hauls necessary? This work is an attempt to present some preliminary answers to such questions.

Earlier sampling had resulted in the adoption of a standard beach seine design. The net measured 60 feet along the lead and cork lines. Mesh size, stretched measure, was 1¼ inches in the wings and ¾ of an inch in the bag. The net tapered from 120 meshes at the ends of the wings to 195 meshes at the center. The bag was 12 feet deep. Sufficient weights were attached to the lead line to cause the net to sink and fish along the bottom at any depth.

The present study considers repeated hauls made with two new nets built to the above specifications. The two beach seines, 60 and 120 feet in length, differed only in the length of the wings. The longer net (net 120) exceeded the shorter net (net 60) by 30 feet of wing length on each side. The longer wings continued to taper slightly, in accord with the design of the net.

The area of Puget Sound under study lies within the Seattle city limits, just south of Meadow Point. The section of beach sampled exhibits a uniform slope from the upper limits to a point below mean lower low water. The slope then increases perceptibly, so that a net set 200 feet from the zero tide point touches bottom in water about 20 feet deep. The intertidal area is uniformly sandy, with small patches of eel grass, *Zostera*, present in the lowest reaches. Past data provided an indication of species and numbers to be expected in the collections.

The first hauls for this study were made on April 26, 1952. The nets were set and hauled simultaneously, each fishing the same strip of beach six times. The paired hauls were made each half-hour from 1½ hours before low tide to 1 hour after low tide. Low tide, —1.8 feet, occurred at 12:06 o'clock.

The manner of fishing and position of each net over its strip of beach were maintained as constant as possible. Hauling lines were approximately 200 feet long, with slight adjustments being made to compensate for tidal changes. The longer net required at least 2 additional men, and was beached about 1 minute after the shorter net.

A second series of collections was made on May 14 and 15, 1952. On May 14, net 120 was centered on the position occupied by net 60 in April. On May 15, net 60 was fished where net 120 had been used in April. The paired hauls of April are given identical letter designations (*e. g.* Table I, 60A and 120A). In May, since the nets were not hauled simultaneously, each haul is lettered in series.

COMPARISON OF NETS

The data accumulated in April reveal a marked contrast in the performance of net 60 and net 120. The total catch included representatives of 25 species of fish. The long net took 24 species, while the short net captured only 18 species (Table I). Furthermore, the first two drags of the long net accounted for 23 species, while two drags of the short net contributed only 12 species. The total number of specimens taken in six hauls is also revealing: 258 in net 120 and 125 in net 60. The 104-pound total weight taken by net 120 is strikingly greater than the 13 pound total taken by net 60.

The hauls taken in May, not being simultaneous, are less dependable for assessing the relative performance of the two units of gear. However, with respect to species, specimens, and pounds of fish caught, the longer net again appears to be definitely superior to the shorter net. In both

[1] This study was made possible by State of Washington Initiative 171 funds for research in biology and medicine. The authors wish to express their appreciation to students in the 1952 class in "Ecology of Marine Fishes" for their assistance in accumulating the data presented.

TABLE I. *Fish collected by 60-foot and 120-foot beach seines, April and May, 1952.*

Net, Date and Haul	Total Specimens	Total Species	Cumulative Species	Weight (lbs.)
60; April 26				
A	23	6	6	1
B	30	9	12	2
C	11	8	16	1
D	11	7	17	1
E	21	5	17	1
F	29	7	18	7
Totals	125	..	18	13
120; April 26				
A	69	15	15	28
B	79	17	23	40
C	28	8	23	8
D	20	9	23	6
E	18	7	23	10
F	44	13	24	12
Totals	258	..	24	104
120; May 14				
A	119	16	16	196
B	98	18	26	20
C	34	11	26	20
D	26	10	27	7
E	17	6	27	3
Totals	294	..	27	246
60; May 15				
F	131	11	11	4
G	37	9	15	7
H	68	14	20	21
I	27	7	21	3
J	30	7	21	6
Totals	293	..	21	41

April and May, five hauls with the short net took six fewer species of fish than were taken in five hauls with the long net. More than 20 percent of the species found in the long net, therefore, were absent from the catch of the short net. Stated in still a different way, it may be said that two hauls with the long net yielded more species than five or six hauls with the short net. Further, the short net, although hauled throughout the period of low water, never equalled the catch of the long net.

Records show that an earlier model of the short net was capable of taking all but one of the species taken by net 120 in this study. The data available suggest that a given strip of beach such as that sampled by the short net does not contain a full representation of the fish population in the immediate vicinity. However, the shortcomings of net 60 as a sampling instrument could produce the same results.

The length-frequency distributions include too few observations to justify analysis. The large variation in the catch of different species seems meaningful. The total catch of each species encountered during the simultaneous hauls of April is tabulated for each net (Table II).

TABLE II. *April catches grouped by seine. Species are listed by order of abundance in the longer net.*

Species	Specimens	
	Net 120	Net 60
Taeniotoca lateralis	59	6
Parophrys vetulus	49	58
Lepidopsetta bilineata	47	10
Damalichthys vacca	23	1
Chitonotus pugetensis	13	4
Platichthys stellatus	12	9
Pholis laetus	9	1
Leptocottus armatus	8	6
Pleuronichthys coenosus	8	5
Syngnathus griseo-lineatus	6	7
Citharichthys stigmaeus	5	2
Apodichthys flavidus	3	2
Aulorhynchus flavidus	2	..
Blepsias cirrhosus	2	4
Cymatogaster aggregatus	2	1
Sebastodes sp.	2	1
Artedius harringtoni	1	..
Artedius fenestralis	1	..
Liparis fucensis	1	..
Microstomus pacificus	1	..
Odontopyxis trispinosus	1	1
Oncorhynchus gorbuscha	1	6
Oncorhynchus kisutch	1	..
Psychrolutes paradoxus	1	..
Enophrys bison	..	1

It is apparent that those species missed by one net form a minor numerical part of the catch of the other net. The seven species peculiar to the collections of the long net comprise over 25 percent of the species captured, but less than 2.5 percent of the total specimens landed. Six of the seven species involved are known to be weak swimmers, and their scarcity in the samples must reflect a similar scarcity on the strip sampled. The seventh species, silver salmon, *Oncorhynchus kisutch,* represented by a single 109 mm. yearling, is an active swimmer. Net 120 also produced a sea-run cutthroat trout, *Salmo clarkii,* a species never captured by 60-foot nets in past sampling. The capture of the salmonids indicates an increase in catching power with wing length.

The single occurrence of the buffalo sculpin, *Enophrys bison,* in the catch of net 60 may reflect a local discontinuity of that species. The May series presents similar evidence as to the minor numerical importance of specimens peculiar to one net.

The dominant species in the long net are represented in the catch of the short net, but the order of abundance differs. Additional simultaneous collections will have to be made with the nets

in order to assess the significance of the deviations. It seems obvious that the short net is not collecting a representative sample, but further collections with a still longer net must be made in order to evaluate net 120.

Effects of Repeated Seining

The data in Table I give evidence of a declining catch as successive hauls are made over the same strip of beach. Any consideration of this problem must recognize factors which complicate the interpretation of the limited data available. Successive hauls did not always cover exactly the same strip of beach as the prototype. Deviation from the original course of the net could easily cause an apparent recruitment to the area of sampling, thus masking any reduction in the catch from the area under study.

Depletion of the strips sampled may have been due to several causes. The unusual activity in the area might disperse some of the more active and wary species. The capture of a school of any species is sufficient to give a distorted impression of the change in species composition. For example, in the May sample of net 60, more than one-half of the specimens in haul F were 45 mm. young-of-the-year pink salmon, *Oncorhynchus gorbuscha*. No other haul in May by either net produced a single additional specimen of this species.

Other complications from schooling may arise. The dominant species in haul 120A in May was the schooling Pacific cod, *Gadus macrocephalus*, which comprised 48 percent of the catch by number and over 75 percent by weight. This fish is a predator upon many of the smaller species which must be depended upon to contribute the basic data for the present study. Such a group of predators might lessen the catch of other species by precipitating their temporary dispersion from the area sampled or by causing them to hide within the area.

Some criterion was sought for evaluation of the change in catch during a series of hauls. A rough measure of the change may be obtained by averaging the results of the first two hauls for comparison with the average of the rest of the hauls made during a series. The catch of the longer net reveals a consistent and impressive difference between the early and late averages of both series.

Evaluated by the same system, net 60 exhibits a less conspicuous reduction in catch of the later hauls of a series. Greatest differences are noted in the total numbers of specimens taken. The reduction in number of species is small in each case, and the average poundage increases during the late hauls.

If the indication of depletion by the large net can be accepted as valid, it is not surprising that the short net yields less distinct evidence of the phenomenon. Difficulty in sampling an identical strip of beach each haul and the narrowness of the area both tend to obscure the true situation. It is apparent that if both nets were out of position by the same number of feet, the short net would fish a greater proportion of new territory.

The possibility of repopulation of the sampling area is present, and the smaller area will presumably return to the original condition more rapidly than the larger area. The action of the net and lines roiling the bottom may even induce fish to enter the area to feed. Considering factors which tend to mask depletion, it appears that the smaller the area sampled the shorter the duration of the effects and the more difficult their detection.

Summary

Two beach seines, varying only in wing length, have been used to make series of collections under closely comparable conditions. The longer net presented a more complete sample than did the shorter net.

With the longer net as a standard, the shorter net took only 48 percent of the specimens, 75 percent of the species and 12 percent of the poundage in the simultaneous series. The occurrence of larger and more active fish in the longer net indicates again that the short net does not capture a representative sample of the fish fauna.

Species taken in only one net are an almost insignificant numerical contribution to the total catch. The occurrence of species represented by a single individual is thought to be an indication of their scarcity in the area. An even longer beach seine must be used to assess the value of the sample obtained with the 120-foot net.

A definite diminution of the catch throughout the series was apparent. The lesser decline in the catches of the short net is probably due to the small area sampled.

THE FORESTS OF ITASCA IN THE NINETEENTH CENTURY AS RELATED TO FIRE

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After 1803, the Lake Itasca region in Minnesota was visited every few years, apparently beginning with William Morrison in that year (Brower 1893). Beginning with Henry R. Schoolcraft in 1832, a series of travelers, journalists, and surveyers interested in the source of the Mississippi River, have left detailed accounts of their observations on the lake and its surroundings. From these, a fairly accurate and detailed picture may be drawn of the forests of Itasca State Park as they were before the establishment of the park in 1891 and the logging of portions of the park between 1902 and 1917.

The single outstanding impression is that most of the park was burned over periodically during the nineteenth century, and that there is every reason to believe that periodic fires had been common in previous centuries. Garrison (1881) graphically describes the typical condition when he climbed a tree a quarter-mile south of Elk Lake in 1880 and wrote:

> For many miles in all directions but the north the surface was gently rolling, none of the hills appearing to be more than twenty or twenty-five feet high; they were chiefly covered with a young growth of birch, aspen and a few oak. Towering above them were seen the black pines (*i.e.*, jack pine) not killed by fires, and an occasional single tree or small groves of Norway pine, towering still above these. These fires which so devastate and utterly ruin so many thousand acres of large pine forests are said to be set by the Indians, purposely, and assisted to spread, to kill the timber, and so give better feeding ground for the moose and deer which abound in this vicinity.

The present-day stands of jack pine (*Pinus banksiana* Lamb.) and red (Norway) pine (*P. resinosa* Ait.) owe their establishment to the clearing of ground by these fires, and their continued existence to their ability to withstand the fires once they reach large sapling size. Figure 1 shows an 18-inch red pine, 227 years old, 4 feet above the ground. It stood north of the Park Drive west of Elk Lake in Sec. 16, and was blown down in the July, 1951 storm. It is representative of the oldest age class of red pine in the park, one which apparently originated after a great fire about 238 years ago or in 1714. This particular tree exhibits fire scars which can be dated from the annual rings at 1772, 1803, 1811, 1820, 1865, and 1886. From sections such as this, from increment borings, and from the records of early observers, the fire and forest history of the tract can be detailed.

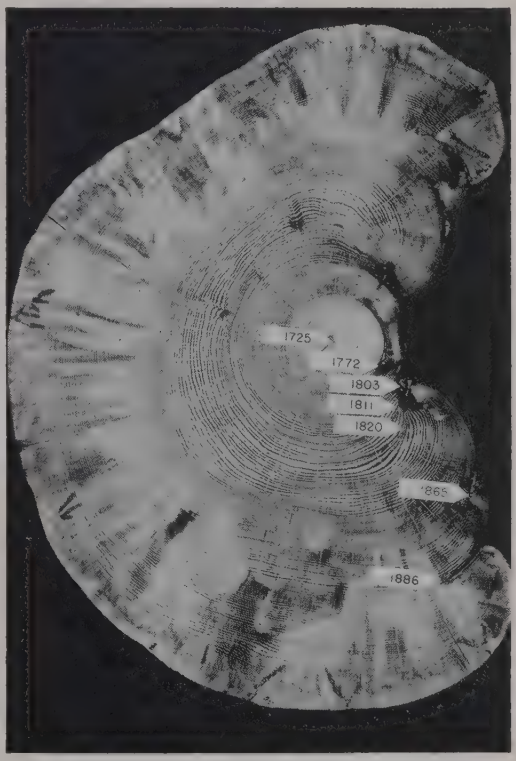

FIG. 1. Cross-section of 18-inch red pine (*P. resinosa* Ait.) showing dating of major fires. This tree from Section 16 west of Elk Lake is 227 years old, about 4 feet above the ground.

Throughout the park are old red pine trees ranging from 215 to 235 years old at breast height. These may be found in Preacher's Grove, at Peace Pipe Springs, along the park entrance road, east of Mary Lake, west of Deming Lake, at Nicollet Cabin, along the Park Drive west of Elk Lake, along the Bohall Trail, and along the Park Drive north of Bohall Lake. No older trees were found in the Park although such trees very likely exist.

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We can conclude with fair certainty that an extremely severe fire (or a series of fires) swept through the entire park about 1714. Of the stands that followed this fire, only the long-lived red and white pines (*P. strobus* L.) still persist.

Several minor fires apparently occurred during the latter part of the eighteenth century. The 1772 fire recorded in Figure 1 is also evidenced by fire scars in the Peace Pipe Springs area and red pine stands now 146-168 years old at breast height. These occur mostly in the northeast portion of the park (east of park headquarters, along LaSalle trail, Peace Pipe Springs), but are also found mingled with the older and younger age-classes along the Park Drive, west of Elk Lake. The rather wide range of ages, coupled with a few records of slightly older and slightly younger trees, suggests the possibility of several minor fires during this period rather than a single major conflagration. Almost any fire in the pre-colonial forest, however, would be expected to burn a sizable area since only swamps and bare land formed natural fire breaks.

The early nineteenth century saw three major fires, in 1803, 1811, and 1820. These, either singly or in combination, gave rise to the major present-day stands of red pine. This age-class (or classes) occurs both as extensive pure stands or mixed with the 230-year age class which followed the 1714 fire. Timber following the 1803, and to some extent the 1811, burn (the 135-age class) makes up the impressive stands around Bohall Lake, northwest of Bohall Lake were the 5-acre sample plot is situated, and in extensive stands west of Hernando de Soto Lake, around Morrison Lake, and west of Whipplè Lake.

Timber following the 1820 burn (the 120-year age-class) is mixed with the 230-year-age-class and also forms pure stands in the area between the park entrance and Mary and Twin Lakes; in the tract west of the southwest corner of Lake Itasca and west of Elk Lake; and in scattered remnants throughout the southest quarter of the park. In the age-class, too, are to be found the oldest remnants of black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*P. glauca* (Moench.) Voss.), and jack pine. The decadence and the dropping out of these species on upland sites is well-illustrated by the records of the 5-acre plot in Sec. 4 (SE-SE), located in the post-1803 or 135-year-old red pine type.

The great majority of the older pine in the park, therefore, originated either after the 1714 burn (or burns) or after the three fires in the first part of the nineteenth century (1803, 1811, 1820). Much of this timber has survived to the present day, despite at least two later severe fires, and makes up the stands for which the tract is presently famous.

When Henry R. Schoolcraft spent 3 hours on Lake Itasca in 1832 and identified it as the source of the Mississippi, he described the forests briefly. He reached the southeast corner of the lake near the present site of Douglas Lodge by portaging from Lake Assawa (Lake Alice), 4 miles to the east-northeast. His description of this portage (1834) may be compared with that of Nicollet (1843) who traversed it in 1836.

Schoolcraft: "The portage from the east to the west branch of the river, is estimated to be six miles. Beginning in a marsh, it soon rises into a little elevation of white cedar wood, then plunges into the intricacies of a swamp matted with fallen trees, obscured with moss. From this, the path emerges upon dry ground. It soon ascends an elevation of oceanic sand, having boulders, and bearing pines (*Pinus banksiana*, according to 1855 version, ed.).

Nicollet: "The first mile of portage is over a short swamp which is succeeded by a small elevation, covered with white cedars and the American Larch; next is a hollow filled up with fallen decayed trees, the accumulation of years and covered with a thick layer of wet moss and other parasites. It is a buried forest, over which another is growing. We left this hollow and reached a sandy country, thinly covered by very small pines . . . the last three miles being over a succession of ascents and descents, between which were most commonly sloughs. The soil is sandy and gravelly, overspread with erratic blocks; but there is a great variety of evergreens, and they are larger than in the (Leech Lake) region mentioned.

Schoolcraft describes the forests around Lake Itasca in general terms, while Nicollet had very little to add:

From the 1834 edition: "The waters (of Itasca) are transparent and bright, and reflect a foliage produced by the elm, lynn, maple, and cherry, together with other species more abundant in northern latitudes. . . . We found here (on Schoolcraft Island), the forest trees above named growing promiscuously with the betula and spruce."

From the 1855 edition: "The diluvial hills inclosing the basin (of Lake Itasca) are covered with pines. From these elevations the lands slope gently down to the water's edge, which is fringed with a mixed foliage of deciduous and evergreen species."

Nicollet: "They (the heights of lands above the lake) are covered with thick forests, in which the coniferous plants predominate."

Still a third traveler, Charles Lanman, visited the area briefly in 1846, without adding materially to our knowledge of the forests.

After these early travelers, severe fire occurred in 1865. This fire is the one noted by Garrison

in the quotation given above. It is also recorded in Figure 1, and in increment borings of the Peace Pipe Springs stands and from the west side of the north arm of the lake (in the 5-acre plot). This fire gave rise to an extensive 75-year-old class (as of 1952), and is also the first fire to be clearly recorded by contemporaneous records.

In 1871, Julian Chambers (1910) visited Lake Itasca and noted that the promontory between the east and west arms was covered with large trees (the west shore of the east arm had "the finest timber between Itasca and Bemidji Lake") with traces of forest fires. The area east of the east arm was covered with young aspen.

The General Land Office survey of the section lines of the area, conducted by Edwin S. Hall in 1875 and in 1879, details the worst burned areas. The original survey notes show severe burns at the north end of the lake, east of the east arm, and between the two arms of the lake. For example, the country along the section line just northeast of present Douglas Lodge is described as, "Burnt land; soil poor 2nd and 3rd rate; timber dead and fallen; pine, aspen and birch; dense undergrowth of hazel, aspen and alder."

Garrison in 1880 added comments on the fire in addition to his quotation given earlier. He noted that "the western shore of the lake is badly burned, with but a few pine trees standing, and dense new growth of birches and aspens among the fallen trees make it a very difficult tract to traverse. The eastern is much less devasted by fire."

The 1865 fire, then, apparently burned through most of the park. It seems to have removed all timber in large tracts east of the east arm, around the outlet to the north of the lake, and between the east and west arms.

The last of the great fires occurred in 1886. This fire was most severe in the northeast section of the park where it has given rise to thousands of acres of 55-year old jack pine and aspen. It is recorded from the west shore of the east arm where it seems to have destroyed the beautiful timber described by Chambers. Finally, its scar is found on the section in Figure 1 and also on others from elsewhere in the western part of the park.

Following the establishment of the park in 1891, fire protection was inaugurated about 1894. The various reports of the Commissioner reveal that no fires occurred in the bad season of 1894 or in 1895, 1896, 1900 and 1901 (Browner 1904). Fires have occurred in the twentieth century in the northeast corner of the park, to the east of Hernando de Soto Lake, and in one or two other localities.

Most of the present merchantable timber in the park stems from four periods and owes its origin to fire. The oldest (about 230-years) pine came in about 1714. The next age-class of pine (135 years) dates from fires in 1803 and 1811. Closely following is the 120-year-old age class following the fire of 1820. The fire of 1865 is clearly recorded both by contemporary writers and by the 75-year-old age class. Finally, the 1886 burn gave rise to the very large acreage of 55-year-old timber, especially on the east side of the Lake.

The dates of the fires assigned above are approximate and may be slightly off. The 1714 date is thought to be within 4 or 5 years of the correct date. The dates for the later fires are probably correct within one year. A detailed study of the fire history of Itasca Park is well warranted and should prove very fruitful.

The records of the nineteenth century forests also provide interesting informaiton of the vegetation of Schoolcraft Island and the general distribution of forest trees in 1875. Schoolcraft Island, because of its prominent position, has been repeatedly visited, described, and photographed. Schoolcraft's own description has already been cited. Dr. Houghton, of the same expedition collected botanical specimens from this spot in 1832, a record of which is attached to Schoolcraft's narrative. Nicollet in 1836 spoke of the island as "covered by a full growth of northern trees, that give it quite a picturesque appearance." Between this time and 1871, however, the forest was destroyed (possibly by the fire of 1865) for Chambers in the latter year described it as covered with underbrush. In 1891, Browner states that the island was covered with a dense growth of birch, basswood, aspen, fir and diamond willow, one stately white pine, and an occasional bur oak.

Another area that was repeatedly visited was the forest south of Elk Lake. The various writers repeatedly characterize this forest as being unusually dense, and it is shown thus on several of the early maps. The hill on the neck of land between Elk Lake and Itasca, however, was clear for many years after the 1865 burn and was so characterized by Garrison in 1880 and Clarke in 1886.

The 1875 G.L.O. survey provides information on the forest at that time inasmuch as some 384 witness trees were measured and described (Table I). Such a tally is invariably weighted in favor of the more durable and longer-lived trees (*i.e.*, the pine and the oaks) as these trees

are preferred for witness trees. The summary table, therefore, serves to emphasize how little of the tract was covered by large old-growth trees at this time, and how often the surveyor had to utilize aspen, paper birch, or dead trees. At two points, two and three-inch aspen were used as witness trees; and at about ten points, no witness trees or only one or two small trees were found.

TABLE I. *Witness trees cited in G.L.O. survey of Itasca Park, 1875 and 1897*

Species	Diameter (inches)						All
	1-4	5-9	11-14	20-24	25-29	30 plus	
Live trees							
Jack pine	3	53	29	1			86
Red pine		16	26	20	11	1 1	75
White pine	1	14	20	9	4	1	49
Pine (undesig.)			1				1
Spruce		5	3				8
Balsam fir	1	5					6
White cedar		2	1				3
Tamarack	2	15	10	2			29
Aspen	16	31	30	1	2		80
Balsam poplar			1	1			2
Paper birch	4	14	6	1			25
Ash	1	3					4
Elm		5					5
Red oak		1					1
White oak		2					2
Oak (undesig.)		3					3
Maple		3					3
Basswood		2					2
Total - live							384
Dead trees							
Jack pine		3	1				4
Red pine				4			4
Aspen			1				1
Paper birch			1	1			2
Total - dead							11

In contrast, two large aspens, 20 and 22 inches in diameter, were used at the southeast corner of Sec. 12 on the Clearwater-Hubbard County line.

In closing the account of the forests of Itasca in the nineteenth century, the course of settlement and logging can be briefly considered. An Indian settlement near the present Indian mounds had been abandoned before white man visited the region. A cabin was built near Nicollet Springs (the site of present Nicollet Cabin) in 1884 to secure timber claims, but was soon abandoned. Peter Turnbull built on the east shore of the east arm in 1883 and a man named Green built just west of present Douglas Lodge before 1887. By the time the park had been established a few years, however, all of these claims were abandoned or had been purchased by the state. The only permanent settlement in the park was built east of the river source by William McMullen in 1889.

In the winter of 1901-1902, the first logging on the park was undertaken, designed to clear up timber blown down in Sections 35 and 36 (145-36) in August, 1900. In this, a logging dam was built across the river at the outlet of Itasca Park. The dam was enlarged in 1904, flooding both Itasca and Elk Lakes. A lumber camp was built on the east shore of the east arm about this time and logged considerable standing timber from the park. Much of the private land within the park boundaries was eventually logged before title passed to the state. The two west tiers of sections in the park were in this category and are not considered as part of the park in the above discussion.

From the standpoint of park management, the condition of the forests of Itasca in the nineteenth century is important. Presumably, the purpose underlying the protection of the park is to maintain an area of the pre-settlement pine forest of Minnesota. This forest was the product of, and has been maintained by, fires which have periodically burned through the area. In a very real sense, fires were part of the normal scene in the pre-settlement forest. Complete protection of the park timber from fire will eventually greatly reduce or even eliminate the pine stands which owe their existence to fire and will replace them with a climax forest composed of spruce, fir, maple, basswood, and other hardwoods. Such a forest will not be representative of the nineteenth century or earlier forest, nor will it be as scenic or as well-suited for recreation as the present pine forest. If the pine forests of Itasca are to be maintained, there are only two alternatives: first, fire may be used as a prescribed and controlled silvicultural tool to regenerate cut-over areas to pine; second, substitutes must be found to do the task accomplished by fire in the virgin forest. Such substitutes would include chemical and mechanical treatment of the brush, followed by scarification of the soil and planting. These procedures would be far more expensive than the controlled use of fire but should accomplish the same ends.

SUMMARY

From the records of early visitors to the region and from examination of tree sections for fire scars, the status of the forests of Itasca State Park in Minnesota during the nineteenth century is described. The present pine stands in the park are due to periodic fires during that and preceding centuries. If these pine stands are to be per-

petuated rather than replaced by boreal or hardwood forests, it is recommended that prescribed burning or some chemical or mechanical substitute be used to prevent this replacement.

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THE ECOLOGY OF THE SPIDERS OF MARITIME DRIFT LINES

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Introduction

Naturalists and ecologists have long been aware that the dead debris washed ashore by large bodies of water supported a rich fauna. However, there have been no published reports of an ecological study of this habitat nor even a list of the fauna found in maritime drift on the western shores of the Atlantic Ocean. The few accounts of drift line studies in this country (Snow 1902; Needham 1904; Herms 1907; Ruthven 1911; Shelford 1913) have all been made on the shores of Lake Michigan.

The only reports in the literature of maritime drift fauna have been by European workers. Keys (1918) and Yerbury (1919) both studied the Plymouth shores of Great Britain and list only a few of the drift line forms as being typical beach animals of that region.

Backlund (1945) made an intensive study of the wrack fauna of Sweden and Finland. Although certain aspects of this habitat are similar, it should be pointed out that the Baltic wrack is not strictly comparable to the familiar drift lines of the sand beaches. The habitat with which Backlund was concerned consists entirely of marine algae that have been tossed up on the rocky shores of Scandanavia. This algal deposition forms banks which after a period of decomposition become peat-like at the lower depths. In addition to detailed environmental studies, Backlund carried out quantitative sampling of the wrack fauna with particular reference to the arthropod population.

In all studies of drift fauna in this country spiders have been completely ignored with the exception of Lowrie's (1948) study of the succession of spiders back from the Lake Michigan shore to the climax forest in which he listed the common beach and drift species. However, spiders are extremely abundant in both maritime and lake drift and such habitats are frequently cited in taxonomic and distributional literature on the group.

The purpose of this investigation was to determine the population structure of the spiders of maritime drift lines and the relationship of that structure to the limiting environmental conditions of the habitat.

The study was carried out at Beaufort, N. C., seventy miles south of Cape Hatteras. The large number of bays and estuaries in this region make possible a wide selection of drift habitats under varied environmental conditions.

The authors wish to express their appreciation to Dr. I. E. Gray for constant guidance and suggestions, and to the Duke Marine Laboratory for the many facilities extended during the course of the investigation.

Habitat

One of the characeristic features of maritime areas is the intertidal zone. In the Beaufort region the difference between mean low and high tide is approximately 2.5 feet. Consequently, the width and extent of the intertidal zone depends on the slope of the land at the water's edge.

This zone, on shores with a very gradual slope and a mud-silt substratum, has been invaded by the grass, *Spartina alterniflora*. If, on the other hand, the slope is steeper and the substratum is sandy a typical beach results. The sand beaches which border sounds or estuaries are termed "closed" or "protected" and are usually quite narrow. In contrast to these narrow beaches those along the ocean are very wide and are termed "open" since they are subjected to direct wave action.

Regardless of whether the intertidal zone consists of a heavily vegetated strip or a sand beach there is always a narrow strip of debris just above the high tide mark which will be termed in this paper the "drift line." This same strip of debris has been called "jetsam" or "flotsam" by other workers. The debris is deposited only by the spring tides occurring twice monthly at new and full moon; rarely do the daily high tides reach the drift line or contribute to the deposition of drift.

Spartina Drift Line. The thickest and widest deposition of debris occurs in those areas in which the intertidal zone is covered with *Spartina alterniflora*. This grass averages three and a half feet in height at low tide level and becomes somewhat shorter as it approaches high tide level. Just above the high tide mark, and with a rise in soil level of only a few inches, there is a very abrupt transition from *Spartina alterniflora* to *Spartina patens*. The drift line always forms the line of demarcation between these two grasses (Fig. 1).

FIG. 1. A *Spartina* drift line forming the point of transition between the *Spartina alterniflora* (right) and *Spartina patens* (left) zones.

Because of the dense nature of the grass the spring tides are never able to push the drift into the zone of *Spartina patens*, even though flooding may extend into this zone. This results in the drift line being nearer the high tide mark than on sand beaches and in some cases the water may even be in contact with the lower margins of the drift.

FIG. 2. Protected sand beach along west margin of Piver's Island. Drift line here consists of small isolated patches of straw and wood.

This type of drift line varies from two to five feet in width and from one-half to two feet in thickness. The debris consists largely of dead *Spartina* straw with pieces of wood interspersed. Decaying fruits and vegetables, paper and other evidences of civilization may sometimes be present.

During this investigation two *Spartina* drift lines were studied: one was located along the southwestern margin of Piver's Island and the other around a small marsh island at the mouth of the Newport River.

Sand Beach Drift Line. The drift line on a sand beach differs markedly from that in *Spartina* in that it is rarely over two feet wide and is only a few inches thick. Since flooding extends above the high tide mark during spring tides and there are no vegetational barriers the drift line is located much further back from the high tide mark than that found in *Spartina*. In many cases it does not form a continuous line along the beach but consists of isolated pieces of driftwood and thin patches of straw. This is especially true of drift lines on an open beach (Fig. 2).

The only difference between drift lines on open beaches and those on closed beaches is one of degree. Far less debris is deposited on the open beach and the little which is deposited is soon buried by the shifting sand. This covering of the drift by sand results in an even less distinct drift line than that found on a protected beach.

Two protected sand beach drift lines and one open beach drift line were studied during this investigation. Both closed beach drift lines were located on Piver's Island, one being on the southwestern margin and the other on the southeastern margin of the island. The open beach drift line was located on Bogue Bank, one of the many outer banks in this region.

METHODS

External environmental conditions existing under the drift and those outside the drift were re-

corded over several twenty-four-hour periods. During this time temperature, humidity, evaporation rate, wind velocity and light intensity were recorded either every hour or every two hours. With the exception of one eighteen-hour recording taken on the open beach all environmental studies were restricted to the southeastern margin of Piver's Island.

Temperatures were taken with standard dial soil thermometers and a whirl psychrometer was used for determining humidities. Since it was impossible to whirl the psychrometer under the drift it was placed on the soil surface and after five minutes the wet-dry bulb readings were recorded; sand-surface humidities were determined in a like manner. In order that all recordings be comparable air humidities were determined by holding the instrument shoulder high for five minutes before recording.

Anderson (1936) has shown that vapor-pressure deficit is more significant than relative humidity and that the actual amount of water vapor present has little, if any, influence upon evaporation. He states that the importance of atmospheric moisture lies in the relation between the amount of water vapor present and the amount that could exist under the same conditions without condensation. This difference between the actual amount of water vapor present and the amount present at saturation point at the same temperature is termed "vapor-pressure deficit." In view of this, relative humidities were converted into vapor-pressure deficits and recorded in mm of mercury.

Standard white and black-bulb Livingston atmometers attached to graduated tubes were used for determining relative evaporation rates. Atmometers placed outside the drift were twelve inches above the surface while those under the drift were level with the soil surface. Evaporation rates were also recorded every fourth day throughout June 1952.

Sampling of the spider fauna was carried out in all five of the drift lines investigated. The sampling methods consisted of shaking drift over a white sheet and turning over boards (hand sampling), Berlese funnel collections, pitfall sampling, and collecting with a headlight at night.

Two methods were used to obtain quantitative data on the spider populations of the drift: hand sampling and pitfall sampling. The size of the unit sample was determined by means of a species: area curve (Oosting 1950, p. 45) in both types of quantitative sampling. A sampling unit was established as fifteen minutes of collecting time.

Wide-mouth bottles, 6 cm in diameter, were used as pitfall traps. These were sunk into the soil under the drift in such a manner that the lip of each bottle was level with the soil surface. The bottles were half-filled with 50% alcohol and drift replaced over their tops. Each bottle remained open in this position for 24 hours. A sample unit was established as the combination of two bottles.

Specimens from each sample were kept separate, identified, and counted; the data obtained were recorded in graphic form with frequency plotted against density of each species. Frequency as used here, refers to the percentage of times a certain species occurs in a certain number of samples and density to the average number of a certain species per sample unit.

Specimens of all species of spiders reported in this work have been deposited in the collections of the American Museum of Natural History.

Results

The Environment

Temperature. The drift debris was found to produce a very marked depression of the soil temperature beneath and also to reduce the amount of temperature fluctuation. On June 17, 1952, a typical summer day, the sand beach temperature was 22°C higher than that under the *Spartina* drift and 18°C higher than that under the sand beach drift at the hottest part of the day (Fig. 3). At night there was a rapid drop from the high mid-day temperatures and by early morning all temperatures were approximately equivalent.

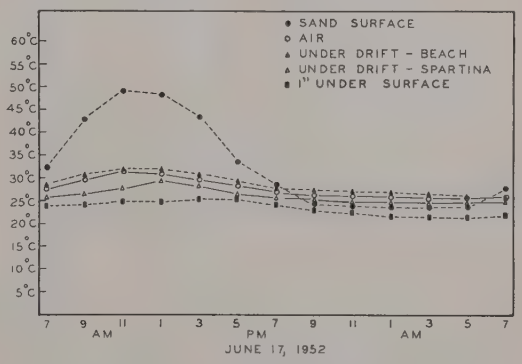

Fig. 3. Temperature variations on Piver's Island on a summer day.

The primary difference between the *Spartina* and sand beach drift lines was one of degree. During the summer the former was always slightly below air temperature while the latter was always slightly above it; however, neither approached the mid-day extreme of the exposed beach sand. During the winter and early spring temperatures be-

neath both types of drift always remained below air temperature.

Vapor-Pressure Deficit. The vapor-pressure deficit of the atmosphere under the drift was consistently lower than that of the surrounding beach sand, *i.e.,* the atmosphere a few inches above the ground under the drift contained more water than that a few inches above the exposed beach surface.

The same general comparison can be made for the vapor-pressure deficit of the air and that under the drift; however, at mid-day the vapor-pressure deficit under the sand beach drift exceeded that of the air for a short period of time (Figs. 4 and 5).

Here again the difference between the *Spartina* drift and the sand beach drift was one of degree, the former having a significantly lower vapor-pressure deficit than the latter.

In the winter and spring the vapor-pressure deficit beneath both types of drift remained lower than that of the air.

Evaporation and Light. As would be expected from temperatures and vapor-pressure deficits the evaporation rate under the drift was also lower than that outside the protection of the drift. During the winter the total evaporation for twenty-four hours outside the sand beach and *Spartina* drift was 19.1 cc and 18.5 cc respectively. However, the bulb under the sand beach drift evaporated only 10.24 cc while that under the *Spartina* drift had a total of only 3.86 cc for the same length of time.

Black bulbs were used in addition to the white for the spring and summer recordings. A comparison between the two bulbs is significant in view of the fact that a white surface reflects light while a black surface absorbs light; therefore, if no light penetrated the drift both bulbs should show the same amount of evaporation.

On April 12, 1952 the difference in evaporation between the two bulbs outside the sand beach drift was 11.16 cc while that between the bulbs under the sand beach drift was only 2.91 cc. In both cases the black bulb showed the highest rate of evaporation. The amount of water lost by the two bulbs outside the *Spartina* drift and those outside the sand beach drift was approximately the same. However, the difference in evaporation between the two bulbs under the *Spartina* drift was less than 0.5 cc. This would indicate that there is a sharp reduction in the amount of sunlight which penetrates the drift and that the *Spartina* drift is almost impenetrable.

During the summer the same general picture was obtained; however, there was an even more marked contrast in the two bulbs under the sand beach than was found during the spring. The black bulb under this drift had a total of 19.41 cc of water lost by evaporation and the white bulb had 15.10 cc. The bulbs under the *Spartina* drift showed no significant difference; the black evaporated 4.51 cc and the while 4.16 cc (Figs. 6 and 7).

In June 1952 evaporation readings were taken every four days above and below the drifts. The

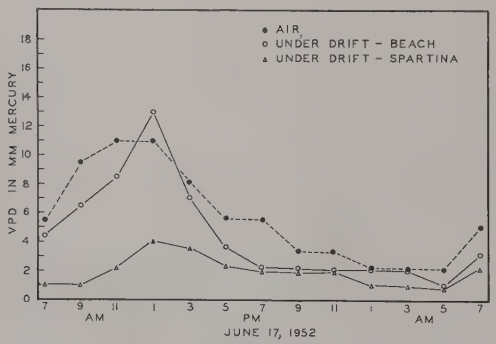

Fig. 4. Variations in vapor pressure deficit on Piver's Island on a summer day.

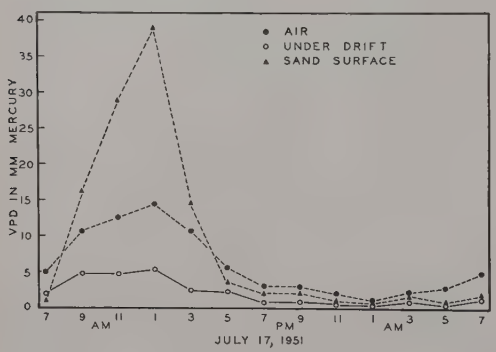

Fig. 5. Variations in vapor pressure deficit on Piver's Island on a summer day.

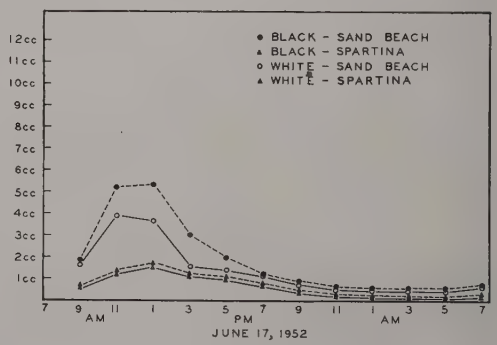

Fig. 6. Evaporation rates under the drift on Piver's Island on a summer day.

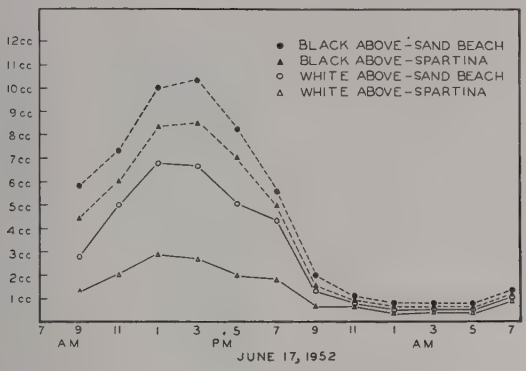

Fig. 7. Evaporation rates over the drift on Piver's Island on a summer day.

results of these data shown in Figure 8 indicated quite clearly the relationship of the amount of light which penetrates both types of drift.

In this series bulbs were placed six inches above the surface of the soil outside the drift in addition to the bulbs twelve inches above. There is a reduction in the evaporation rate as the bulbs approach the sand surface (Fig. 9). The black bulb twelve inches above the surface lost a total of 1969 cc during the 28 days while that six

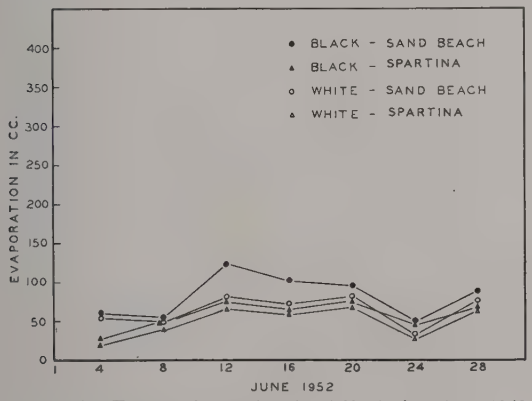

Fig. 8. Evaporation under the drift during June 1952 on Piver's Island.

inches above lost 1565 cc. However, the black bulb under the sand beach drift lost only 563 cc and that under the *Spartina* drift evaporated 385 cc.

Wind Velocity. Wind velocity during this study usually varied between two and eight miles per hour; the highest recorded was fifteen miles per hour. This mild breeze would contribute to the evaporation rates on the beach but probably would not contribute to any great extent to those under the drift. Winds strong enough to move any of the debris were never observed.

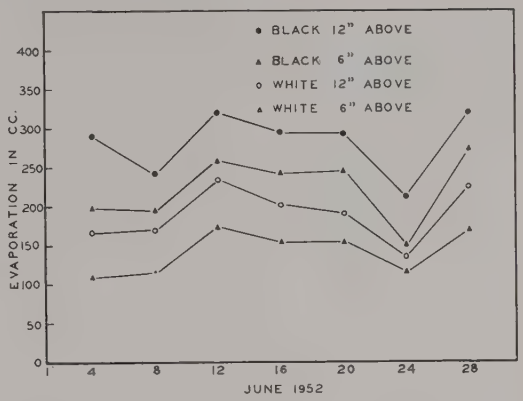

Fig. 9. Evaporation over the drift during June 1952 on Piver's Island.

pH of the Soil under the Drift. An attempt was made to measure the pH of the soil under the drift with a LaMotte Soil Testing Set. The extent of color indicators in this set is 8.2 which was found to be too low to obtain a color reaction with the soil. Therefore, it can only be said that the pH of the soil under the drift was more alkaline than 8.2.

Comparison of Conditions on an Open and a Closed Beach. Temperature, vapor-pressure deficit, evaporation rate and wind velocity were recorded over a eighteen-hour period on an open beach on Bogue Bank and at the same time on a protected sand beach on Piver's Island. Both air and sand surface temperatures on both beaches declined rapidly after mid-day and fell below air temperature at night.

Vapor-pressure deficits on Piver's Island were also lower than those on Atlantic Beach although this comparison had to be restricted to the air since this factor was not recorded beneath the drift on the open beach. Although the vapor-pressure deficit beneath the drift on the protected beach became slightly higher than that of the air it always remained lower than the vapor-pressure deficit of the air on the open beach.

The Spider Fauna

A total of thirty-six species of spiders belonging to eleven families and twenty-nine genera were collected in the Beaufort maritime drift lines. This total represents not only quantitative but also non-quantitative sampling from the five drift lines investigated. All species collected are listed in Table I.

Spartina Drift Line. All quantitative sampling for the determination of population structure in *Spartina* drift was carried out in the drift line surrounding a small island at the end of a series

TABLE I. *Species of spiders taken in the maritime drift lines, at Beaufort, N. C.*

	Spartina	Protected	Open
Pholcidae			
Psilochorus pullulus (Hentz)			X
Theridiidae			
Latrodectus mactans (Fabricius)		X	
Paidisca marxi (Crosby)		X	
Linyphiidae			
Tennesseellum formicum (Emerton)		X	
Micryphantidae			
Ceraticelus anomalus Gertsch		X	
Eperigone banksi Ivie and Barrows		X	X
Erigone autumnalis Emerton	X		
Grammonota sclerata Ivie and Barrows		X	
Grammonota trivittata Banks	X		
Argiopidae			
Singa keyserlingi McCook	X		
Lycosidae			
Arctosa furtiva Gertsch	X		
Arctosa littoralis (Hentz)		X	X
Lycosa carrana Bryant	X		
Lycosa modesta (Keyserling)	X		
Pirata suwaneus Gertsch	X		
Schizocosa salsa Barnes	X	X	
Trochosa shenandoa Chamberlin and Ivie		X	
Gnaphosidae			
Drassyllus adocetus Chamberlin	X		
Gnaphosa sericata (L. Koch)		X	X
Poecilochroa capulata (Walckenaer)		X	
Poecilochroa unimaculata (Emerton)	X		
Clubionidae			
Clubiona littoralis Banks	X		
Clubiona nicholsi Gertsch	X		
Clubiona plumbi Gertsch		X	
Meriola decepta Banks		X	
Micaria sp.		X	
Scotinella pintura (Ivie and Barrows)		X	
Thomisidae			
Misumenoides formosipes (Walckenaer)		X	
Salticidae			
Habronattus agilis (Banks)		X	
Habronattus calcaratus (Banks)		X	
Hyctia bina (Hentz)	X		
Metacyrba taeniola (Hentz)		X	
Onondaga lineata (C. L. Koch)	X		
Peckhamia picata (Hentz)	X		
Dictynidae			
Dictyna gloria Chamberlin and Ivie		X	

of salt marshes extending north of U. S. 70 between the Beaufort and Morehead bridges. The spider population of this drift line is represented in the frequency-density diagram shown in Figure 10 and was based on ten fifteen-minute hand samples (Table II). Two of the samples were taken in May and August 1951 and the remainder in May and June 1952. This population was composed of only twelve species and had a density of 17.8, *i.e.*, 17.8 spiders per sample. *Lycosa modesta* comprised the largest part of the population, its density of 9.9 was slightly more than half of the total. *Clubiona nicholsi* and *Poecilochroa unimaculata* both had frequences of 80 per cent but their densities were far smaller than those of *Lycosa modesta.*

Of the twelve species collected only two, the little ant-mimicking spider, *Peckhamia picata,* and

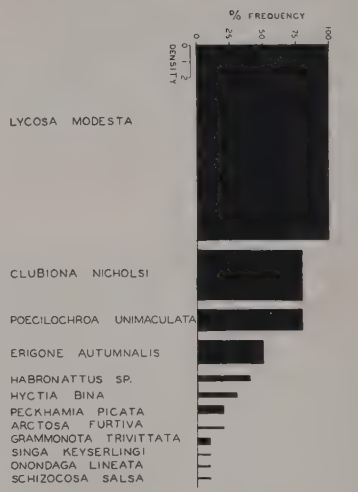

FIG. 10. Frequency-density diagram of the spider population in a *Spartina* drift line at mouth of Newport River estuary.

Clubiona nicholsi, were never found out of this particular habitat. The other species were collected in the communities on either side of the drift line.

Lycosa carrana, a large wolf spider, was not taken in this series of drift line samples but a number of specimens were collected with a headlight at night in 1951.

Ordinarily the *Spartina* drift line is quite damp but during prolonged dry periods in the summer of 1951 the drift became noticeably dry. Several samples were taken when the drift was in this condition and the spider population had markedly decreased.

Although only qualitative samples were taken in the *Spartina* drift on Piver's Island, the species

TABLE II. *Composition of ten samples taken in* Spartina *drift at the mouth of the Newport River estuary.*

	May 31, 1951	August 13, 1951	May 19, 1952	June 15, 1952	June 15, 1952	June 15, 1952	June 15, 1952	June 15, 1952	June 15, 1952	June 15, 1952	Density	Frequency
Lycosa modesta	1	28	9	13	16	9	3	10	2	8	9.9	100%
Clubiona nicholsi	1	2	3	..	9	5	4	6	..	1	3.1	80%
Poecilochroa unimaculata	2	2	1	1	..	1	1	2	..	5	1.5	80%
Erigone autumnalis	..	..	4	..	..	2	1	3	..	1	1.1	50%
Habronattus sp.	..	1	1	..	1	1	..	..	..	..	.4	40%
Hyctia bina	..	..	..	1	1	1	..	..	..	..	.3	30%
Peckhamia picata	..	4	..	..	..	..	..	..	..	1	.5	20%
Arctosa furtiva	..	..	..	..	..	..	..	..	1	1	.2	20%
Grammonota trivittata	..	..	5	..	..	..	..	..	..	..	.5	10%
Singa keyserlingi	..	..	..	..	..	..	..	..	..	1	.1	10%
Onondaga lineata	..	..	1	..	..	..	..	..	..	..	.1	10%
Schizocosa salsa	..	..	..	..	..	..	..	..	..	1	.1	10%
Total	4	37	24	15	27	19	9	21	3	19	17.8	

which were collected and the relative abundance of each closely approximated the preceding quantitative samples.

All drift lines are subjected to complete flooding several times a year. A small area of *Spartina* drift observed one night in May 1952 during a very high tide showed that the tangled straw was not covered by the high water, which extended even into the *Spartina patens,* but floated in a mass on the surface while the surrounding grass prevented anything but vertical movements. The headlight reflected the eyes of many little wolf spiders running over the mass of floating straw; when they were disturbed they disappeared down into the debris.

Protected Sand Beach. The drift line of the protected sand beach of Piver's Island was found to have a strikingly different spider population than that found in *Spartina* drift. It might be reiterated that this type of drift line is made up of solitary pieces of wood and small isolated patches of straw, all of which were frequently partially covered by sand. Two fifteeen-minute hand samples were taken in July and August 1951 and the remaining eight were taken in May and June 1952 (Table III). Sixteen species were collected and the total density was 9.1 individuals per sample (Fig. 11). Four species, *Gnaphosa sericata, Clubiona plumbi, Grammonota sclerata* and *Micaria* sp., made up over two-thirds of the population. *Gnaphosa sericata* had the highest frequency and density of the four major species. *Clubiona plumbi, Grammonota sclerata* and *Micaria* were about equal in density although *Micaria* had a lower frequency. *Clubiona plumbi,* a small

TABLE III. *Composition of ten samples taken in protected sand-beach drift on Piver's Island.*

	July 23, 1951	August 27, 1951	May 18, 1951	May 18, 1951	June 10, 1952	June 10, 1952	June 17, 1952	June 17, 1952	June 19, 1952	June 19, 1952	Density	Frequency
Gnaphosa sericata	..	..	2	3	2	..	5	4	6	8	3.0	70%
Clubiona plumbi	1	1	..	..	..	..	3	..	4	3	1.2	50%
Grammonota sclerata	..	3	2	..	..	..	2	4	..	1	1.2	50%
Micaria sp.	2	3	..	..	..	3	..	2	..	..	1.0	40%
Eperigone banksi	..	..	..	..	2	..	4	..	..	..	.7	30%
Arctosa littoralis	..	..	..	..	1	..	1	..	2	..	.4	30%
Habronattus calcaratus	1	1	..	..	..	..	..	..	..	..	.2	20%
Habronattus agilis	..	..	..	..	..	1	..	1	..	..	.2	20%
Schizocosa salsa	..	..	..	..	..	..	1	1	..	..	.2	20%
Tennesseellum formicum	..	..	..	..	1	3	..	..	..	..	.3	10%
Castianeira sp.	..	..	..	..	..	2	..	..	..	..	.2	10%
Poecilochroa capulata	..	..	..	..	..	..	..	..	1	..	.1	10%
Misumenoides aleatorius	..	..	..	..	..	..	..	..	1	..	.1	10%
Aysha gracilis	..	..	1	..	..	..	..	..	..	..	.1	10%
Metacyrba taeniola	..	..	1	..	..	..	..	..	..	..	.1	10%
Scotinella pintura	..	..	..	..	..	1	..	..	..	..	.1	10%
Total	4	8	6	3	6	10	16	12	14	12	9.1	

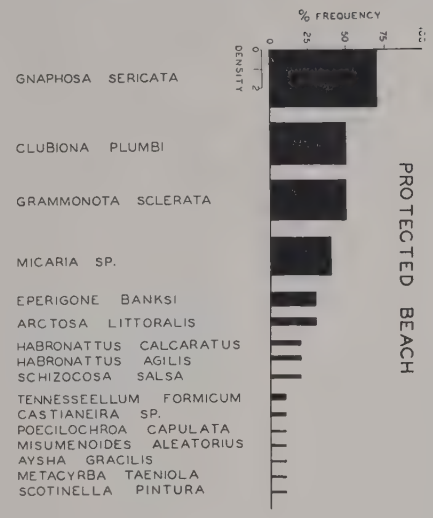

FIG. 11. Frequency-density diagram of the spider population in a protected sand-beach drift line on Piver's Island.

cursorial spider, and the little web-building micryphantid, *Grammonota sclerata,* were largely restricted to the patches of drift straw while *Gnaphosa sericata* and *Micaria,* both cursorial forms and the latter an ant-mimic, were just as abundant under pieces of wood. This was particularly true of *Gnaphosa sericata;* even small pieces of wood a few inches long would harbor one or two individuals of this species.

Two other ant-mimicking spiders besides *Micaria* were collected in this drift line, *Tennesseellum formicum,* a little linyphiid, and an unknown species of *Castianeira.* A number of specimens of the large micryphantid, *Eperigone banksi,* were collected beneath pieces of wood. This same species was also collected on the protected beach of Shackleford Banks beneath dried cattle dung.

Although *Arctosa littoralis* had a low frequency and density in the drift line, this nocturnal wolf spider was extremely abundant on the beach at night. A headlight revealed many individuals running over the sand, particularly in May, June and July. During low tide these spiders would range down over the wet sand near the water's edge and a number were observed feeding on the little crustacean, *Talorchestia.* The very immature individuals of this species hide during the day under the drift straw and wood while the adults and penultimate instars burrow in the sand.

Drift Line of Open Beach. The drift line of the open beach was investigated on Bogue Bank at Fort Macon Beach where the greatest amount of drift was present. Ten fifteen-minute hand

samples were taken, two in July and August 1951 and eight in June 1952 (Table IV). In order to take these samples almost every piece of driftwood and straw was examined over a two mile stretch of beach. Five species were collected and the total density was 2.8 individuals per sample (Fig. 12). The major part of the population was made up of *Arctosa littoralis* and *Gnaphosa sericata*.

TABLE IV. *Composition of ten samples taken in open sand beach drift on Bogue Bank.*

	July 31, 1951	August 8, 1951	June 30, 1952	June 30, 1952	June 30, 1952	June 30, 1952	June 30, 1952	June 30, 1952	June 30, 1952	June 30, 1952	Density	Frequency
Arctosa littoralis	6		2	2	1	4	1		1		1.7	70%
Gnaphosa sericata	1	1		1		1	1	2			.7	60%
Micaria sp.		1				1					.2	20%
Eperigone banksi						1					.1	10%
Psilochorus pullulus						1					.1	10%
Total	7	2	2	3	4	5	2	2	1	2.8		

Arctosa was the more abundant of the two but all of the individuals collected were immature. The remainder of the population consisted of three species: *Micaria* sp., *Eperigone banksi* and *Psilochorus pullulus*. Two specimens of *Micaria* were collected and the other two species were represented by single specimens.

MIGRATION FROM THE DRIFT

An attempt was made in June 1952 to determine (1) the degree of migration by the spider population out of the drift and (2) the difference in activity during night and day.

In order that these data might be placed on a quantitative basis, twenty pitfall traps were placed outside the drift between the high-tide mark and the drift line and twenty beneath each type of drift. This made a total of eighty traps, twenty in each location.

Each group of twenty was then subdivided into two lots, half of which were opened from 7:00 a.m. to 7:00 p.m. and the other half from 7:00 p.m. to 7:00 a.m. All traps remained in place for forty-eight hours after which they were removed and the contents determined.

The results of this series of samples are shown in the graph in Figure 13. Only the total number of spiders collected in each of the ten traps is given because of the small species totals in most of the series.

DISCUSSION

Allee *et al.* (1949, p. 436) have defined a major community as a "natural assemblage of organisms which, together with its habitat, has reached a sur-

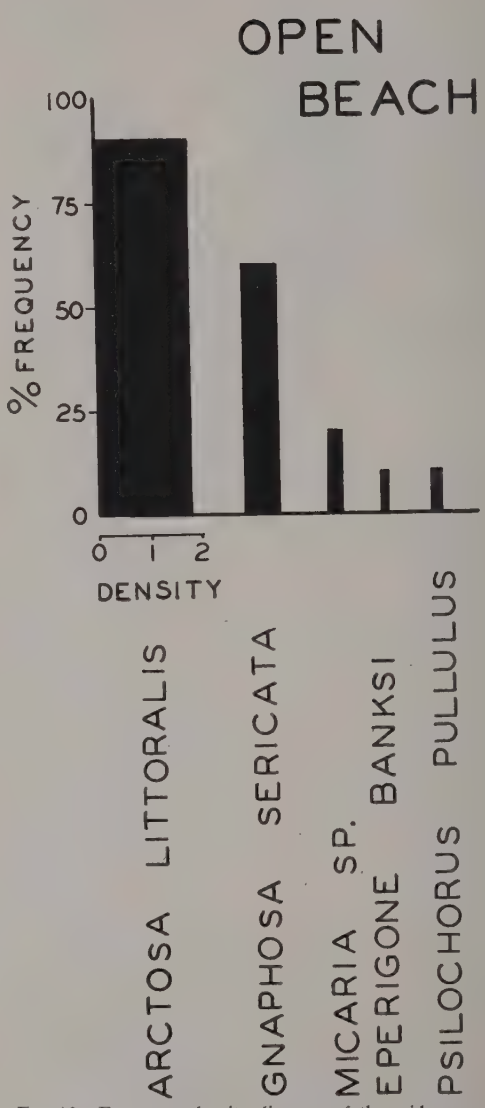

FIG. 12. Frequency-density diagram of the spider population in an open sand-beach drift line on Bogue Bank.

vival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent, given radiant energy, it is self-sustaining."

It will immediately be seen that the drift line does not qualify as a major community. It is not independent of the adjacent communities nor self-sustaining but derives energy from the debris of adjacent communities (*Spartina alterniflora, S. patens,* the sea).

Despite the fact that both types of maritime drift lines are formed in the same manner and are,

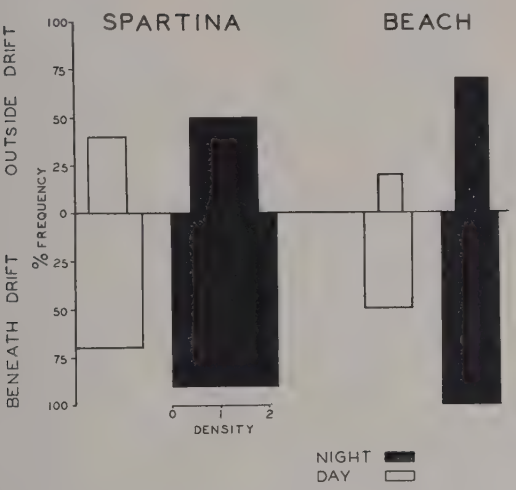

FIG. 13. Comparison of the activity of the spider population beneath and outside of the drift during day and night on Piver's Island.

therefore, quite similar in structure, the microclimate of each is strikingly different.

The environment beneath *Spartina* drift is distinctly mesic with a subdrift temperature, vapor-pressure deficit and evaporation rate below that of the air above the drift. The microclimate of sand beach drift is, in contrast, quite xeric. All of the microclimatic factors here are higher than those beneath *Spartina;* temperatures and vapor-pressure deficits may even exceed that of the air. It is significant, however, that although the sand beach has a xeric microclimate it is well below the climatic extremes found on the bare exposed sand outside the drift and remains within the range of toleration for many forms of animal life.

The microclimatic character of both *Spartina* and sand beach drift is ultimately dependent on two factors (1) the thickness of the drift and (2) the degree of vegetation over the adjacent soil surface. In general, the thicker and heavier the deposition of drift and the more heavily vegetated the adjacent areas the more mesic will be the subdrift environment. Conversely, the thinner and more sparse the drift and the less vegetated the adjacent soil surface the more xeric the environment will be.

It will immediately be seen that it is actually these two physical characteristics that differentiate *Spartina* and sand beach drift lines.

The *Spartina* drift line has a very thick deposit of drift straw. It has already been shown that this heavy mass of debris greatly depresses the subdrift temperature, vapor-pressure deficit and rate of evaporation beneath it. Furthermore, a comparison of the evaporation rates of black and white atmometer bulbs indicates little or no light penetration.

The relatively thin drift on the sand beach does not depress the subdrift temperature, vapor-pressure deficit or evaporation rate to as great an extent as does *Spartina* drift. A comparison of white and black atmometer bulbs showed that a significant amount of light penetrated the drift. The high mid-day temperature and evaporation rate of the adjacent exposed sand would tend to lessen to some extent the ameliorating effect of the drift here.

The difference in the microclimate of *Spartina* and sand beach drift lines is strikingly reflected in the two totally different spider populations which each supports.

The spider population of the sand beach drift lines are characterized by xeric species such as *Gnaphosa sericata, Clubiona plumbi, Grammonota sclerata, Micaria* and others. However, all of these species require the protection of the drift for survival. The spider assemblages of open and closed sand beaches are actually the same, but the more extreme environment of the open beach results in a far lower population density for that habitat than for the drift line of the protected beach. Perhaps the chief reasons for the smaller population of spiders on the open beach are the smaller amounts of drift present and the constantly shifting sand which frequently covers the little wood and straw present; spiders were rarely found under deeply buried driftwood. Roughly the same amount of drift which was distributed over three hundred yards of protected beach on Piver's Island was distributed over two miles of beach at Fort Macon.

The drift line of the protected beach contained a number of ant-mimicking species: *Castianeira* sp., *Micaria* sp. and *Tennesseellum formicum. Micaria* was so similar to a small red ant also present that it was frequently difficult to distinguish between them.

Immature *Arctosa littoralis* were present in the drift on both the open and closed beaches but were more abundant in the drift of the open beach. Despite frequent night searches with a headlight no adults were found outside the drift on the open beach, whereas the protected beach supported a large population of adults. This seems to indicate that immatures of this species have greater toleration for unfavorable environmental factors than do adults.

This strictly nocturnal spider was reported by Lowrie (1948) to be one of the most abundant species of the beach and drift on the southern shore of Lake Michigan. Table V compares the spiders

found by Lowrie on the beach at Lake Michigan with the characteristic species of the protected maritime beach at Beaufort.

TABLE V. *Comparison of the spiders of the Lake Michigan beach drift and the maritime beach drift at Beaufort*

Lake Michigan (Lowrie 1948)	Beaufort (Barnes and Barnes)
Arctosa littoralis (Hentz)	*Arctosa littoralis* (Hentz)
Pardosa milvina (Hentz)	*Gnaphosa sericata* (L. Koch)
Pirata piratica (Olivier)	*Clubiona plumbi* Gertsch
Schizocosa avida (Walckenaer)	*Grammonota sclerata* Ivie and Barrows
Crustulina altera Gertsch and Archer	*Micaria* sp.

With the exception of *Arctosa littoralis* no species is common to both habitats. *Arctosa* is the only wolf spider prevalent in the sand-beach drift at Beautfort whereas four of the five Michigan species are wolf spiders.

In contrast to the xeric spider population of the sand beaches that of the *Spartina* drift is distinctly mesic. With the exception of *Schizocosa salsa* there is not a single species which is common to both types of drift. *Arctosa littoralis* is replaced by a member of a related genus, *Lycosa modesta,* in the *Spartina* drift and *Clubiona plumbi* is replaced by a closely related species, *Clubiona nicholsi.*

While the *Spartina* drift line does not contain as many species as does the drift line of the sand beach, its population density is twice as large. The moist environment of *Spartina* drift also supports more species of wolf spiders than that of the sand beach. In addition to the very abundant *Lycosa modesta, Lycosa carrana* and *Arctosa furtiva* were also present. The drift is undoubtedly an important breeding site for *Lycosa modesta* since many immatures of this species were found here throughout the year.

Cursorial spiders made up by far the most important part of the population in both types of drift lines and except for the xeric *Grammonota sclerata* the Micryphantidae were rare. On the other hand, Backlund (1945) found the Micryphantidae extremely abundant in the Baltic wrack both in species and numbers; although wolf spiders were also prevalent the other cursorial groups composed only a small part of the spider fauna. This is undoubtedly correlated with the structure of the wrack habitat which, despite its algal origin, is more similar to forest litter than to the types of drift habitats described here.

The spider populations of these two types of drift lines show very distinct relationships to certain other maritime communities which have similar microclimates. The spider fauna of the sand-beach drift line is very similar to that found in the xeric dune grass community. The majority of the species in the drift line were also present in the population living in the bases of the dune grass; two of the characteristic drift-line species, *Clubiona plumbi* and *Grammonota sclerata,* were also characteristic species of the Uniola community (Barnes 1952).

The *Spartina* drift fauna, on the other hand, is more clearly related to that of the adjacent *Spartina patens* community and in many respects should be considered a transitional zone between the two *Spartina* communities. With the exception of *Peckhamia picata* and *Clubiona nicholsi,* all of the species found in this type of drift were also found in the two adjacent communities. All of the wolf spiders were also members of the *Spartina patens* community, while *Poecilochroa unimaculata* and *Hyctia bina* were members of the *Spartina alterniflora* community. The few specimens of *Grammonota trivitata* and *Singa keyserlingi* taken in the drift should not actually be considered members of the habitat, but rather as accidental vagrants from *Spartina alterniflora.*

In both types of drift there is a significant amount of migration of the spider population out of the drift line. This conclusion, of course, is based on the assumption that pitfall sampling carried out in this study is an accurate measure of the activity of the spider populations. This may not yield a strictly accurate picture and it is no doubt subject to some error, but certainly some activity can be measured in this manner. Since the bottles were placed between the high-tide mark and the drift line it is reasonable to assume that all individuals which migrated out of the drift would eventually be forced to return.

The greatest amount of migration out of the drift occurred at night. This might be expected since at this time the environments under the drift and outside the drift most closely approximate each other. As the sand surface temperature rises on the exposed sand surface and conditions in general become more unfavorable the majority of the migrating population undoubtedy returns to the drift line. The larger migration which takes place out of the *Spartina* drift line is only a function of the larger population which the *Spartina* drift supports.

The beach fleas, *Talorchestia,* which appear in large numbers on the beach at night may be a factor in the migration of the spiders out of the drift. These little crustaceans are important prey of the spider population. Pitfall sampling indicated that while they are always present beneath the drift, migration onto the beach occurred only during the night.

Summary

1. The purpose of this investigation was to determine the structure of the spider population of the maritime drift lines at Beaufort, North Carolina and the environmental conditions characteristic of that habitat.

2. The maritime drift lines in the Beaufort area are of two types: *Spartina* drift lines and sand beach drift lines, the latter being found on both open and closed beaches.

3. The thick debris of the *Spartina* drift lines depresses the temperature, vapor-pressure deficit and evaporation rate beneath and results in a stable mesic microclimate.

4. The thin drift of the sand-beach drift line produces a microclimate within the range of toleration of many animals and well below the high extremes of the exposed sand surface. However, the subdrift environment is distinctly xeric in contrast to the mesic conditions beneath *Spartina* drift.

5. The xeric and mesic nature of the two types of maritime drift lines results in each supporting a characteristic but totally different spider population.

6. The spider population of the *Spartina* drift has a greater density than the sand-beach drift but the latter maintains a larger number of species. The characteristic species of spiders found in *Spartina* drift are: *Lycosa modesta, Clubiona nicholsi* and *Poecilochroa unimaculata;* in the sand-beach drift *Gnaphosa sericata, Clubiona plumbi, Grammonota sclerata* and *Micaria* sp. are the most characteristic.

7. The spider population of the sand-beach drift is very similar to that found in the xeric dune-grass community; the spider fauna of the *Spartina* drift, on the other hand, is somewhat transitional in composition between the two *Spartina* communities adjacent to it.

8. The drift populations are not limited entirely in their activity to the drift debris but migrate out of the drift onto the adjacent beach and into the *Spartina alterniflora* areas. This migration, however, takes place largely at night when subdrift and exposed sand-beach environments most closely approximate each other.

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EFFECTS OF SATURATED SOIL ON SEEDLING GROWTH OF SOME BOTTOMLAND HARDWOOD SPECIES

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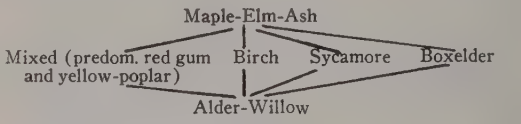
The effects of flooding forest tree roots have been reported variously as being of little or no consequence, or as immediately detrimental to growth. Hunt (1951) subjected pine seedlings to different soil moistures in a range from flooded to wilting percentage and found a very slight differential in growth as a result of treatment at the end of seven months. Parker (1950) reported that flooding the root systems of dogwood resulted in serious injury within a week, but white oak, red oak, and overcup oak survived for several weeks. Kramer (1951) found yellow-poplar quite susceptible to flooding injury in the brief span of two weeks. Hunt, Parker, and Kramer all used potted seedlings that were from one to three years old. Hunt's conclusions were based upon mortality and growth (dry weight), while Parker used transpiration rates as a basis of comparison. Kramer observed mortality, foliar discoloration, degree of wilting, and epinastic manifestations for his conclusions.

Yeager (1949) made a detailed seven-year study of the effects of permanent flooding accompanying hydroelectric development, channel improvement, and flood and erosion control. In his observations of river-bottom hardwoods characteristic of the upper Mississippi River valley, he found that actual flooding (as opposed to just a raising of the water table) of timber areas resulted in practically complete tree mortality. Trees growing vigorously showed the geratest resistance to flooding, while small trees with low vigor and overmature trees were affected in a relatively short time. Yeager reported willow, cottonwood, elm, and silver maple reproduction becoming established on mud flats after most of the original stand (consisting in part of these same species) had been killed. Previously existing reproduction of these species was killed by the impoundment.

Depending on the amount of rainfall, drainage characteristics of the soil, and proximity of the water table, it seems certain that most lowland or drainage areas, if not flooded, would at least be subject to soil saturation of a few days' duration every spring. Yeager suggests a shift from forest vegetation to marsh conditions with permanent flooding, but flooding of relatively brief duration for any one year could be a decisive factor in species composition on bottomland sites if there is a differential in the tolerance to saturation of seedlings of different species.

In his phytosociological studies of the plant communities of the North Carolina Piedmont area, Oosting (1942) includes a comprehensive analysis of the bottomland components. Despite the many irregularities and exceptions to general pattern occasioned by past land use, the general trends indicated in the diagram below, although somewhat oversimplified, appear to typify the dominant communities of secondary succession. This progression from alder-willow to maple-elm-ash is usually a very wet to a moderately wet habitat transition.



In a preliminary attempt to evaluate seedling tolerance to saturated soil as a factor in ultimate stand composition of bottomland communities, species of these three successional levels were selected for study. The species used were hazel alder (*Almus rugosa* (Du Roi) Spreng.), sycamore (*Platanus occidentalis* L.), river birch (*Betula nigra* L.), American elm (*Ulmus americana* L.), winged elm (*Ulmus alata* Michx.), and red maple (*Acer rubrum* L.).

The original view taken in this investigation was that saturated soil conditions would result in seedling mortality, and it was felt that the time in days required to bring about mortality would provide a means of ranking the six species used in comparative order of saturation tolerance. Mortality did not result, and it soon became evident that continuous saturation, while resulting in very conspicuous stunting, did not completely eliminate any species nor did it result in wilting or indications of epinasty. Therefore, an attempt was made to measure the degree of recovery from the stunted condition and in this manner arrive at a comparison of flooding tolerance by species.

Materials and Methods

Seedlings of the size and age indicated in Figure 1 were transplanted into three-inch pots and

[1] The author expresses his appreciation for the advice given by Dr. H. J. Oosting, Botany Department, Duke University, during this study.

the soil was kept at field capacity and above for three days, to permit the seedlings to stabilize before subjecting them to saturation. A light potting soil that had a field capacity of 19.7 per cent and a wilting percentage of 9.9 was used. Despite the differences in age of the seedlings of the six species, it was felt that selecting a stage of comparable development would provide some initial measure of constancy. The seedlings were therefore transplanted to the pots with the appearance of the first true leaves.

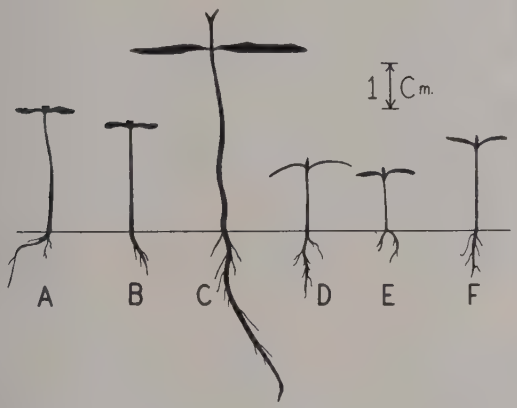


FIG. 1. Seedling sizes at the time of transplanting to experimental pots. A, American elm 11 days old; B, winged elm 12 days old; C, red maple 8 days old; D, sycamore 17 days old; E, alder 12 days old; and F, river birch 12 days old.

Each treatment was applied to 20 seedlings in four pots of five seedlings per pot, and the treatments were 0, 1, 2, 4, 8, 16, and 32 days of continuous saturation.

The pots were placed in galvanized pans and flooded so that the free-water surface in the pots was approximately one-quarter inch below the soil surface and the surface was saturated by capillary fringing. This water level was kept approximately constant by use of hydrostatic heads as shown in Figure 2. The saturating pans were located in an unshaded section of the greenhouse and extreme soil temperatures were recorded. The pots of a species series were numbered and drawn at random from the water. After the pots were drawn from the water they were allowed to drain and were subsequently kept at and above field capacity on a cinder bed. Heights of the plants were measured at the end of 32 days, at 42 days, and at 52 days. These measurements were taken in the latter part of June and early July of 1951, and made possible a comparison of maximum stunting and rate of recovery of all species.

FIG. 2. Galvanized pans containing flooded pots showing the maintenance of the free-water surface by means of hydrostatic heads.

RESULTS

Several statistical comparisons of the results are possible. The main comparison was to see if height growth incurred by seedlings subjected to a "days in water" and "days out of water" schedule was static. Table I is presentation of mean height growth and significant mean differences of the control versus individual treatments. With additional measurements at 32 + 10 days and again at 32 + 20 days, species differences became evident with regard to 32-day standing. These data are presented graphically in Figure 3.

At 32 days, river birch subjected to 1-day saturation showed no evidence of being stunted; all other treatments resulted in significant stunting, and the growth responses evidenced the same effects of treatment at 32 + 10 days and 32 + 20 days. Red maple was stunted by all treatments, except 4 days of saturation at the time of the 32-day and 32 + 10 standings. At the 32 + 20 measurements, however, red maple subjected to 1 and 2 days of saturation and then kept at field capacity and above for 31 and 30 days no longer showed any significant effects, and the 4-day treatment had a stunting effect. Sycamore was significantly stunted by the 32-day treatment, but all other treatments produced no significant differences. The last sycamore measurements at 32 + 20 days showed no alteration of the 32-day status. Saturation of 1, 2, and 4 days' duration had no significant effect on the subsequent growth of American elm, although 4 days proved to be stunting at the time of the next two height measurements. The 8, 16, and 32-day stunting effects on American elm shown in Figure 4 were permanent.

Growth responses of winged elm varied. The 32-day measurements showed a beneficial effect

TABLE I. *Mean height growth of seedlings subjected to treatments of 1 to 32 days saturation compared to mean height growth of control (0) seedlings*

Species	Treatment days							Time of measurement
	0	1	2	4	8	16	32	
River birch	10.52	9.98 ( )	7.46 (−)	7.17 (−)	5.11 (−)	4.11 (−)	5.06 (−)	32 days
Red maple	15.94	14.32 (−)	13.41 (−)	14.86( )	13.42 (−)	10.26 (−)	7.19 (−)	
Sycamore	7.82	8.11 ( )	6.70 ( )	8.40 ( )	7.18 ( )	7.35 ( )	6.28 (−)	
American elm	8.03	8.81 ( )	8.04 ( )	7.42 ( )	6.48 (−)	6.03 (−)	5.95 (−)	
Winged elm	4.38	5.17 (+)	4.21 ( )	4.89 ( )	4.10 ( )	3.01 (−)	2.89 (−)	
Alder	1.75	2.91 (+)	2.94 (+)	3.00 (+)	2.84 (+)	3.16 (+)	3.40 (+)	
River birch	19.94	19.86 ( )	16.77 (−)	14.58 (−)	11.04 (−)	7.38 (−)	9.66 (−)	42 days
Red maple	18.70	16.30 (−)	15.36 (−)	16.58 ( )	15.42 (−)	12.75 (−)	8.34 (−)	
Sycamore	12.56	13.10 ( )	10.34 ( )	12.35 ( )	11.69 ( )	10.82 ( )	9.66 (−)	
American elm	11.83	12.48 ( )	11.80 ( )	9.36 (−)	7.82 (−)	7.41 (−)	7.40 (−)	
Winged elm	8.31	8.75 ( )	7.28 (−)	7.47 ( )	5.96 (−)	3.97 (−)	3.14 (−)	
Alder	2.74	5.42 (+)	4.73 (+)	4.68 (+)	4.39 (+)	4.18 (+)	4.86 (+)	
River birch	24.67	24.50 ( )	21.64 (−)	18.25 (−)	15.45 (−)	12.99 (−)	15.78 (−)	52 days
Red maple	20.30	18.42 ( )	17.44 ( )	17.79 (−)	16.56 (−)	14.18 (−)	10.76 (−)	
Sycamore	14.84	15.42 ( )	12.93 ( )	13.70 ( )	13.79 ( )	12.83 ( )	12.30 (−)	
American elm	17.57	15.77 ( )	15.18 ( )	13.51 (−)	12.02 (−)	11.29 (−)	11.25 (−)	
Winged elm	15.11	15.15 ( )	12.12 (−)	12.57 (−)	10.71 (−)	6.82 (−)	6.18 (−)	
Alder	6.50	10.68 (+)	7.93 (+)	9.14 (+)	7.76 (+)	6.66 ( )	6.30 ( )	

(+) difference from check significantly positive at 5 per cent level, thus increased growth.
(−) difference from check significantly negative at 5 per cent level, thus reduced growth.
( ) no significant difference in growth response.

TABLE II. *Relative degree of recovery after most injurious treatment (min.) compared to recovery after most favorable treatment (max.)*

Species	Treatment	Days	Ht. (cms.) 32 days	% Incr. + 10 days	% Incr. + 20 days	
River birch	maximum	0	10.52	47.24	18.41	Very rapid recovery to stunted growth responses
	minimum	16	4.11	44.30	43.18	
Red maple	maximum	0	15.94	14.75	7.88	Very rapid recovery to stunted growth responses
	minimum	32	7.19	13.78	22.49	
Sycamore	maximum	1	8.11	38.09	15.04	Rapid recovery to slightly stunted growth responses
	minimum	32	6.28	34.99	21.46	
American elm	maximum	0	8.03	32.12	32.63	Moderate recovery to some stunted growth responses
	minimum	32	5.95	19.48	34.31	
Winged elm	maximum	1	5.17	40.91	41.59	Moderate recovery to stunted growth responses
	minimum	32	2.89	8.00	49.19	
Alder	maximum	32	3.40	30.04	22.85	Some saturation growth promoting
	minimum	0	1.75	36.13	57.84	

of 1-day saturation; 2, 4, and 8 days had no apparent effect, and 16 and 32 days of saturation had a negative effect on growth (Fig. 4). In the final analysis of growth of winged elm (at 32 + 20), however, the effect of 1-day saturation was no longer significant and all other treatments were significantly stunting.

Alder presents an interesting contrast in that all saturation treatments promoted height growth, with the exception of 32, which at 32 + 20 days was no longer significant. Graphically (Fig. 3), growth of alder is seen to be greatly increased by 1-day saturation, which is by far the best treatment. The behavior of alder was, to say the least, unique in all respects. Whereas the 32-day treatment of maple, the elms, and birch, resulted in 100 per cent survival and sycamore 95 per cent, alder suffered a 60 per cent mortality, all within the 8-day treatment. Seemingly the individuals that survived beyond this time showed little or no difference in final height growth in a comparison of the 16 and 32-day saturation treatments.

Figure 3 illustrates rather forcibly that river

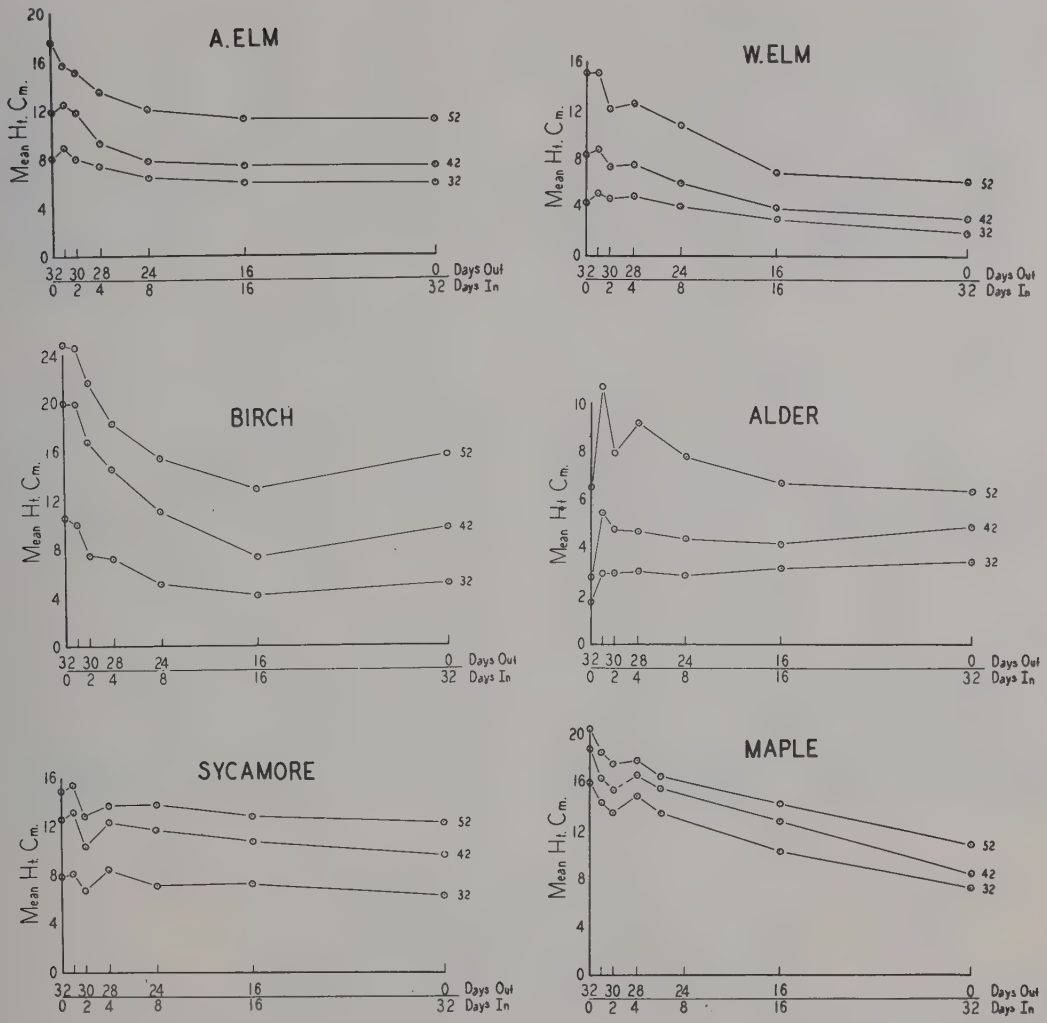


FIG. 3. Mean height growth responses of seedlings subjected to a "days in water" and "days out of water" schedule.

birch made better growth and maintained it at the 32-day treatment than it did after 16 days of saturated soil followed by 16 days of well-drained soil.

The spread of the three lines in each graph is a measure of the relative growth rate of the species under the conditions imposed. If the minimal point, or treatment of greatest stunting, is compared with the treatment of least stunting, or maximum growth, over the two ten-day periods, an indication of relative degree of recovery from stunting may be made. The results of such a comparison are presented in Table II, where the species are listed in the order of their recovery rate.

DISCUSSION

The stunting effects of saturation treatment were similar in all species. Internodes were extremely short, which gave the seedlings a rosette appearance. The cotyledons of the elms yellowed and dropped off earlier in the longer saturation treatments, and in general the leaves of all species were small but not characterized by readily discernible anatomical abnormalities except the size. The pulvini and veins of sycamore were a brick-red color in the 16 and 32-day treatments, but this condition soon disappeared with soil drainage.

Admittedly, reproduction in natural bottomland sites would not likely be subjected to such uni-

FIG. 4. Growth responses at 32 + 3 days saturation to days of continuous saturation, as indicated by the numerals, of American elm seedlings to the left of the numerals and winged elm seedlings to the right of the numerals.

form conditions nor to soil temperatures as high as 37° C as were observed in the greenhouse. These results do indicate, however, the ability of these species to become established after initial germination and subsequent drainage on sites with a high water table and/or soils of poor internal drainage characteristics.

In terms of seedling tolerance to saturated soil conditions as a factor in initial stand composition on bottomland sites, it seems possible that alder occupies wet marshes and the margins of low drainage areas because the growth of seedlings is at least not inhibited by saturated soil. River birch seedlings recover very rapidly from stunting induced by saturated soil and sycamore seedlings rapidly, which may account for their successional position above the extremely wet alder habitat. Winged elm and American elm seedlings recover at a moderate rate and thus their ultimate stand status on sites that are drier than those of sycamore and river birch stands.

Red maple seedlings recover from stunting induced by saturated soil at a very rapid rate. Therefore, this species might be expected to be in the river birch-sycamore successional level. In general, however, red maple is found in the drier elm-ash level and its absence in the more moist habitats is more likely due to seedbed condition limitations or limiting growth conditions after the young seedling stage.

It seems likely that continually saturated soils would almost completely eliminate the tree seedlings due to severe stunting if not ultimate elimination. However, even on soils that drain rapidly after relatively short periods of saturation, damage to the young seedlings by being overtopped by water may be a more decisive mortality factor than soil moisture conditions. Water overtopping damage might be due to washing out or matting down, or a result of curtailment of physiological processes.

Summary and Conclusions

Seedlings of sycamore, river birch, American elm, winged elm, red maple, and alder that had just developed their first true leaves were subjected to saturated soil conditions of varying time intervals followed by intervals of soil moisture at and above field capacity under conditions of approximately one-half sunlight and high soil temperatures. Comparisons of height growth in 10-day periods after the most favorable soil treatment (days) and height growth in 10-day periods after the most stunting soil saturated treatment were made. After subjection to a sustained saturated substratum with subsequent well-drained conditions, river birch and red maple seedlings recover very rapidly, sycamore rapidly, and American elm and winged elm at a moderate rate. The growth rate of alder seedlings is accelerated by short intervals of soil saturation, and their growth is not significantly changed by sustained saturation intervals up to 32 days.

The relative degree of recovery from stunting induced by previously saturated soils of young seedlings of alder, river birch, sycamore, American elm, and winged elm may be indicative of their successional relationships and ultimate stand composition in bottomlands.

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STUDIES ON SUMMIT-FREQUENTING INSECTS IN WESTERN MONTANA[1]

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Introduction

On a warm day in July 1951 the writer climbed Squaw Peak, a rather isolated and rocky summit, 7,996 feet in elevation, some 25 miles northwest of Missoula, Montana (Fig. 1). At the summit surprisingly large numbers of insects, particularly various types of Diptera, were seen flying rapidly about or resting on the bare rocks. This was not expected in view of the barren nature of the summit and the relatively few insects noted in the forest and rock slide areas below. A search in the literature during the following year, for similar observations, revealed only a few brief reports of mountain-top insect abundance. During the summer of 1952 several trips were made to the same peak in order to study this phenomenon and especially to secure evidence that would help to determine whether or not distinct preference for the very top of the mountain was shown by any insects.

Methods

Visits were made to the summit on the following dates: May 10, June 7, 28, July 2, 3, 15, 16, 28, 29, August 3, 8, 9, 26 and September 2. All visits in July and that of August 8, 9 were for

[1] The following persons identified the insect species mentioned in this study: Bombyliidae, W. W. Wirth; Coccinellidae, E. A. Chapin; Cuterebridae, C. W. Sabrosky; Ichneumonidae, L. M. Walkly; Sarcophagidae, H. R. Dodge; Siricidae, B. D. Burks; Syrphidae, C. L. Fluke; Tabanidae, C. B. Philip; Tachinidae, P. H. Arnaud.

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FIG. 1. Squaw Peak as seen from a ridge about eight miles to the southeast.

periods of 24 hours or over, and a total of approximately 70 hours was spent in actual study and collection of insects on and near the summit. Data were primarily secured from three study and collecting stations located as follows: station A, summit; station B, 165 linear feet from A and 24 feet lower in altitude; station C, 173 linear feet from B and 51 feet lower in altitude. Stations B and C, with slopes of 10° and 40° respectively, were located at 290° with reference to A and consequently did not receive direct sunlight as early as A but did receive more radiant energy in the afternoons. The surface at station A consisted for the most part of bare or lichen-covered rocks, but small patches of soil which supported grass, scattered herbaceous plants, and some low juniper shrubs also occurred there. The substratum at stations B and C was entirely made up of rather large lichen-covered rocks. Two cairns, one four and a half feet and the other eight feet high, were located at station A. All stations were several dozen feet from the nearest trees. Figures 1, 2 and 3 give some idea of the nature of the peak and of the collecting stations.

Insects at and near the summit were studied by visual observation and net collection, by trapping them with pans of oil-covered water, by bait fly-traps and by counts of audible evidences of insect flight.

Net collections of insects were intended for the most part only to provide representatives of the species conspicuously present during any period.

FIG. 2. View of station B looking in the direction of station C. Note collecting pan on rocks.

However, enough individuals of some species were taken to permit determination of sex ratios with some validity. Much time was spent in visual observation of insect activity at the three stations, with reference to general behavior and quantitative and qualitative changes in insect populations with time and place.

The pans of water were used in order to secure some degree of objective sampling of insects. Fuel oil was added to the water in order to provide a surface film that would increase the efficiency of insect capture. One large pan and one small pan, 12 x 19 x 2 inches and 16 x 25 x 3½ inches respectively, were placed at each station on June

FIG. 3. Aerial photograph (U. S. Forest Service) of Squaw Peak and vicinity showing extent of rock slide areas. Summit is indicated by arrow. Horizontal distance summit to lake approximately ⅓ mile.

28. At subsequent visits water was added and the insects from the various pans were strained out and placed in 80% alcohol for later sorting and counting.

The fly traps were of a type described by Dodge and Seago (1954). Bait consisted of pig entrails. Two traps were set at each station for approximately 24 hours at the times of the overnight visits. The flies were removed after treatment with DDT aerosol. Used bait was taken at least a mile away from the summit and buried.

The problem of objectively measuring insect activity was met by using activity counts, which were made by sitting quietly in one spot and, with a hand counter, recording each distinctly separate audible buzz due to insect flight of some type. Wind interfered with hearing at times and it was not possible to tell how many buzzes were due to a single particular insect. Also, during the higher levels of activity it was difficult to keep track of all separate sounds heard because of their number. In spite of these limitations it is felt that such counts provided a satisfactory type of activity measure and the consistency of counts made under similar conditions was quite good.

Temperature, relative humidity and wind meas-

urements were made at intervals during the study and collection periods. A glass-bulb mercury thermometer was used for temperature readings. Breast-high air temperature and rock-surface temperature readings were both taken, with thermometer shaded. Relative humidity was determined occasionally by a sling psychrometer. Wind velocity at the 1½ foot level was measured by a portable Taylor anemometer during each activity count and at various other times. No measurements of light intensity were taken although cloud cover was always noted.

Observations and Results

During all study periods a greater number of insects was noted at the summit than at the lower stations or at other lower areas. Repeatedly on approaching the summit from below, regardless of direction, the greatest number of active insects was seen at the very top, considering this region to include the area above a contour line about six to eight feet below the highest point of the summit surface.

A list of those insects that are considered, on the basis of collections and observations, to show definite summit preference is given in Table I. There is little doubt that more intensive studies would place many other species in the list since questionable forms are not included. Table I also gives the sex of those specimens that were identified by specialists. Although many of the species are represented in numbers too small to justify a conclusion as to sex ratio the total picture unquestionably reveals a far greater number of males. Data are not available on the ratios of males to females actually produced by the species represented but it is presumably, at least for the Diptera, about 50:50.

Table I. *Insects observed to prefer summit to adjacent lower areas.*

Species	Number	
	Male	Female
Bombyliidae		
Thevenetimyia sp.	5	2**
Villa sp. prob. *agrippina* (O.S.)	8	0
Coccinellidae		
Hippodamia caseyi Johns.	..	..
Cuterebridae		
Cephenemyia jellisoni Tns.	8	0
Ichneumonidae		
Pseudamblyteles sp. nr. *nuncius* (Cress.)	11	0
Pseudamblyteles animosus (Cress.)	14	0
Sarcophagidae		
Ravina querula (Wlk,)	41	1
Siricidae		
Urocerus flavicornis (Fab.)	27	0
Syrphidae		
Arctophila flagrans O.S.	10	0
Chrysotoxum ventricosum Lw.	8	10
Cynorhina armillata O.S.	14	0
Cynorhina robusta Curr.	8	0
Eristalis tenax L.	36	1*
Sphecomyia pattoni Will.	18	1*
Tabanidae		
Hybomitra rhombica var. *osburni* Hine	9	0
Hybomitra rupestris Mart.	11	1*
Hybomitra zonalis (Kirby)	25	1*
Tabanus aegrotus O.S.	6	0
Tabanus sequax Will.	2	0
Tachinidae		
Fabriciella nitida v.d.W.	31	1*
Gonia porca Will.	4	0
Mochlosoma sp.	9	0
Peleteria conjuncta Curr.	7	0
Peleteria iterans Walker	20	1*

*One mating pair.

Most of the species listed showed a specific pattern of distribution and behavior. A brief description will be given of the activity of some of the most characteristic of the summit-frequenting groups.

The coccinellids were noted at all periods throughout the summer. Individuals could almost always be seen flying around during the warmer days and particularly on the west side of the summit. They would frequently alight on the rocks and crawl around. On June 28 and on September 2 small gatherings of a few individuals each were found under rocks very close to station A. Small collections of dead specimens, from past years, were also noted in this area. The ladybird beetles were not confined in their activity to so small or localized an area at the summit as in the case of most of the other insects listed. Scattered flying or crawling individuals were seen at stations B and C also during the summer but they were not so numerous and no gatherings of individuals were seen at these places.

The deer botfly, *Cephenemyia jellisoni*, was first noted on August 3. Individuals were taken then and again on August 9 and September 2. On the latter date eight specimens were captured and some three hours were spent in observing active individuals. This species was never seen at stations B and C and at station A showed distinct preference for the larger of the two cairns. It was estimated that individuals alighted on this cairn some twenty times more frequently than on the summit surface or on the smaller cairn. For the most part specimens were inactive and rested on the cairn rocks in the sun. However, occasionally they would fly and circle actively with each other or with the larger tachinids for up to 45 seconds and would then return to the rocks. They did not appear to fly any more rapidly than the tachinids or the summit tabanids. No mating activity was noted and no females were taken.

The ichneumonid wasps were frequently present

in such numbers that they could be taken by dozens in one minute by net. Frequently they would concentrate over a patch of low juniper shrubs at station A although scattered individuals would constantly be flying close to the rock surfaces all about the summit. Activity appeared to be almost continuous. They were much less abundant at stations B and C. No activity that suggested a reason for their presence at the summit was noted.

The sarcophagids, of which many species were present although only one is listed as a summit form, undoubtedly accounted for much of the activity count data. Individuals of this group exhibited the most common type of activity noted at the summit, namely rapid circling flight, often in pairs or threes, followed by periods of rest on the warm rock surfaces. They were relatively inconspicuous at stations B and C.

The siricids were present in small numbers, from two or three to a dozen at any one time, but were noted throughout the summer. They would fly over the summit continually with great rapidity, making such wide circles away from the top that they could sometimes scarcely be seen, then returning to dart past the summit again. Their rapidity and range of flight made them difficult to net but when they alighted on rocks, frequently those of the smaller cairn, they were easily taken. None were noted at stations B and C. No mating activity was seen and no females were taken.

The Syrphidae, Tabanidae and Tachinidae could be considered the groups most characteristic of the summit as each had several species showing this type of distribution. *C. ventricosum,* in the Syrphidae, is the only species listed which appears to be represented by as many females as males. *Eristalis tenax* was one of the most abundant of summit species and was present throughout the summer. Specimens were fairly widely distributed about station A and immediate surroundings but were only infrequently seen at stations B and C. The two *Cynorhina* species were observed only on July 28 and 29 but were both abundant on those days and showed distinct summit preference. The Syrphidae listed exhibited much the same type of individual behavior as described for the sarcophagids but also showed some periods of hovering in their flight.

The Tabanidae showed the most hovering activity, so much so that one could not help wondering about their source of energy. It should be noted that with the exception of occasional syrphids none of the insects listed in Table I were seen feeding on or near the summit. The tabanids would hover some one and a half to two feet above the surface for several seconds, then would dart away and return to hover again, frequently at the same spot. Only rarely would specimens rest on the rocks when seen on the summit. No tendency to form even loose swarms was noted although several individuals were active about the peak at the same time on several occasions. No tabanids were seen at stations B and C. A marked tendency towards early morning activity was observed in members of this group. Some specimens would be active by 7:00 a.m., being among the first insects to fly in the morning, and usually by 10:00 or 11:00 a.m. they would be rare or absent. Although females at times caused some annoyance in the forest *en route* to the peak, by biting, the only females noted at the summit were taken while they were mating. Mating in all of the Diptera was detected by a sudden loud buzzing which usually served to locate a flying pair. Sometimes the pair would settle nearby but at other times they would fly away from the summit and out of sight.

Members of the genus *Fabriciella* were the most conspicuous of the Tachinidae. For presumed insect parasites these large black fast-flying flies are surprisingly abundant on high mountain rocky areas in Montana. They appeared to be more numerous at Station A than at B and C but, like the syrphid *E. tenax,* were by no means limited to the summit and were also present throughout the summer. The only female tachinids taken were in mating pairs.

Butterflies of the families Nymphalidae and Pieridae flew around and by the summit during most of the study periods. However, they did not noticeably favor the top of the mountain in their activity. Many insect groups were notably rare or absent on the mountain top. Only two dragonflies were observed during the entire study period and both lingered only a matter of seconds within sight of the summit. No other insect predators were observed there although asilids were frequently seen in areas considerably below the summit. No cerambycids or buprestids were observed at any of the study stations although both were expected to be present at least occasionally in view of the extent of the surrounding forest area. Only on two occasions were mosquitos noted and then only a few individuals were present. Bumblebees were very numerous about the heath and other flowers below the summit but although one would occasionally fly over the station A area, in no case did it hesitate more than a few moments before moving down again.

Alpine grasshoppers were noted on all rock-slide areas near the peak.

In wet open forest glades considerably below the peak many of the insects found on the summit, especially species of the Tachinidae and Syrphidae, were seen frequenting flowers. A small wet meadow with abundant flowers adjacent to the small permanent lake northeast of the peak (see Fig. 3) had a very high insect population during the summer months and many of the summit forms were represented there. However, many other insects abundant here were not seen at the summit. In early summer some five small temporary lakes or ponds may be seen in the same general area. It seems very likely that such areas as have been mentioned, within a mile or less of the peak, furnish most of the summit insects in the sense that they provide suitable soil conditions for immature forms, host material for the parasites and food for many of the adults. The botflies presumably come to the peak from more distant areas.

Some of the data from the oil-water pan collections are given in Table II. Although these pans were left on Squaw Peak throughout the summer they were found to be dry on some of the visits. The water appeared to evaporate more slowly from station B and C pans than from those at station A and because sampling time was probably not constant no quantitative comparisons of trapped insects were made in such cases.

TABLE II. *Analysis of pan-collected insects from stations A, B, and C.*

	June 28-July 3			July 16-July 29			July 29-August 3			August 3-August 9		
	A	B	C	A	B	C	A	B	C	A	B	C
Bombidae	0	5	7	17	11	20	16	4	11	6	1	1
Coccinellidae	72	54	21	43	28	5	110	39	13	21	13	4
Ichneumonidae	56	21	14	345	87	65	453	15	18	220	18	12
Lepidoptera												
Butterflies	17	4	2	21	5	12	60	21	18	17	9	12
Moths	9	5	4	16	18	10	23	18	25	15	14	15
Locustidae	1	0	0	12	0	0	11	0	0	5	0	0
Siricidae	1	0	0	16	0	0	34	3	0	10	0	0
Syrphidae	156	295	319	35	15	33	42	7	49	7	5	21
Tabanidae	0	0	0	2	0	0	0	0	0	1	0	0
Tachinidae	10	13	6	24	4	5	14	4	10	13	6	16
Other insects 6 mm. or above in total length												
Diptera	72	127	75	290	126	136	140	74	100	107	51	70
Hymenoptera	132	145	112	18	37	13	10	32	19	6	11	15
Coleoptera	11	0	5	14	1	4	12	1	3	1	6	2
Hemiptera	0	1	1	3	5	6	1	26	37	0	10	11
Insects smaller than 6 mm. in total length in cc. wet volume*	4.6	2.2	1.0	5.4	1.1	1.3	13.1	3.6	2.3	4.8	2.4	2.5

*August 3 Station A 3.1-cc. sample gave 1129 insects or 364 insects per cc.
August 9 Station C 2.5-cc. sample gave 527 insects or 211 insects per cc.

The pans seemed to sample different insects with different degrees of efficiency as might be expected. Thus *Eristalis,* the tabanids and certain other groups were not so well represented as expected on the basis of their observed numbers. However, the data support the results of the visual observations fairly well for the coccinellids, siricids, and ichneumonids. They also indicate greater abundance of butterflies and grasshoppers at station A than at B and C. With reference to the Syrphidae, it was quite apparent in sorting and counting the insects that the variety of forms taken obscured any indication, by this method, of the summit-frequenting tendency of some of the species. Also, pan collections of *Chrysotoxum* cast doubt on its placement as a summit-frequenting group, for in the July 29-August 3 sample 32 out of 49 syrphids at station C, but only 7 out of 42 syrphids at Station A, were members of this genus.

There is evidence in the numbers of moths, Hymenoptera other than siricids and ichneumonids, and Hemiptera, that some insects are more abundant at lower stations than at the summit, or are at least equally abundant. The six-millimeter total body length, excluding appendages, was selected arbitrarily as a point at which to divide the smaller insects, which are presumably more easily influenced by the wind, from the larger ones. It can be noted that in all collections there were more small insects at station A than at station B or C. Most of these insects were Diptera (cyclorrhaphous types definitely predominating over nemocerous types) with Hymenoptera next in abundance, some Thysanoptera and relatively few Coleoptera and Homoptera.

Fly-trap catch figures (Table III) did not show any constant distribution pattern for insects sampled in this way. The following families were represented in the traps: Calliphoridae, Sarcophagidae. Tachinidae, Muscidae, Syrphidae, Bombidae, Vespidae. The calliphorids were the most numerous, being about five times more abundant than the next group, the sarcophagids, and the other families mentioned were represented only by small numbers. It should be noted that the calliphorids, although present at station A in considerable numbers, did not appear to show distinct preference for the summit.

The activity-count method seemed to have considerable validity as a measure of general insect activity. Wind velocities, time of day and season, air temperature, and cloud cover all influenced the level of activity markedly. Wind velocity was measured during each count and above approximately 300 feet per minute appeared to inhibit

TABLE III. *Numbers of insects taken by fly traps.*

Date and time interval	Max. air temp. during period	Station A	Station B	Station C
July 2-3 (2:00 p.m.) 22 hrs...	18°C	688	110*	1,484
July 15-16 (2:00 p.m.) 22 hrs...	11°C	76	61	23
July 28-29 (4:00 p.m.) 26 hrs...	21°C	447	2,183	414
Aug. 8-9 (2:00 p.m.) 22 hrs.†.	15°C	115	213	114

*One trap only.
†Cloudy during most of period.

activity in proportion to its magnitude (see Fig. 4). Data obtained at stations A, B and C (Fig. 5 is an example) show the differences in activity at these points under very much the same physical conditions of the environment. Activity counts also gave some definite values for the change in insect activity when small clouds blocked the sunlight. For example, six one-minute counts made on August 8 (air temperature 15°C, between 3:30 and 4:30 p.m.) in full sunlight gave an average count of 64 (wind-velocity average for count periods was 41 feet per minute) while during the same period six counts made when the sun was obscured gave an average count of 4 (wind-velocity average for these count periods was 35 feet per minute). The effect of the direct sunlight on activity was marked, particularly for the flies, and a definite decrease in insect flights appeared as soon as ten seconds after the sunlight was cut off, although rock surface temperatures were maintained for several minutes. Differences between air temperature and rock-surface temperature taken at the same time frequently reached 10°C and it was thought early in the studies that the heating of the rock substratum and retention of the heat for some time by it provided a microclimate that was a major attractive feature to summit insects. However, such influence of the direct sunlight on insect activity as noted does not support this idea.

Maximum activity counts were taken on July 29 and ranged up to 124 per minute. The higher air temperatures encountered at the peak (15° to 19°C) appeared to occur at times of maximum insect activity. There was no clear correlation of activity with relative humidity values, which ranged from 30% to 66% at noon during the summer study periods.

DISCUSSION

There are several reported instances where insects have been observed to frequent mountain tops, sometimes in considerable numbers Boie

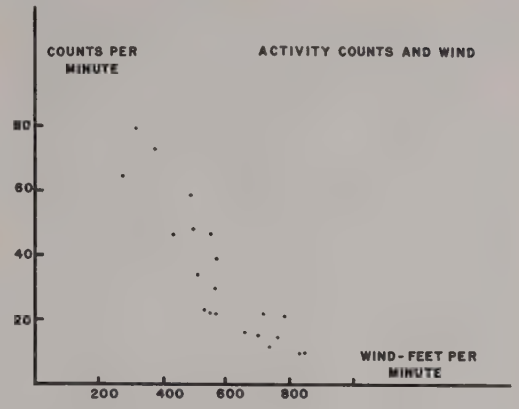

FIG. 4. Simultaneous activity counts and wind measurements made from 5:05 to 5:30 p.m. July 28, at station A.

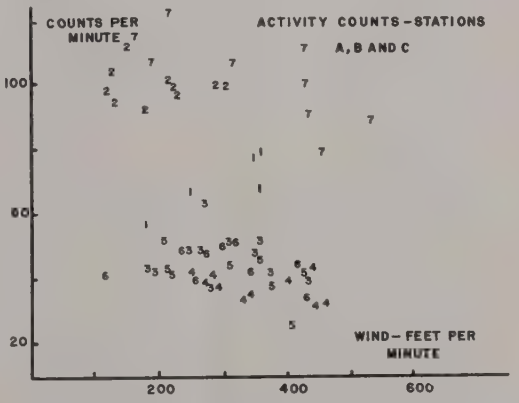

FIG. 5. Activity counts at stations A, B and C, July 29; (1) station A, 6:50 a.m.; (2) station A, 10:30 a.m.; (3) station B, 11:55 a.m.; (4) station C, 12:30 p.m.; (5) station C, 1:00 p.m.; (6) station B, 1:20 p.m.; (7) station A, 1:40 p.m.

(1850) gives some observations of Saxesen on the presence at summits of two species of botflies. According to Brauer (1863) Saxesen was the first to record this type of behavior in these flies. Brauer lists four species of oestrid or related flies as showing a marked tendency, especially in the males, to frequent hill and mountain tops and described the behavior of *Cephenemyia stimulator* in this respect in some detail.

Poulton (1904) discussed the general phenomenon of mountain summit insect aggregations. He cited some degree of insect abundance on peaks as occurring in *Dorcadion* (Cerambycidae), *Ammophila* (Sphecidae) and *Coccinella* (Coccinellidae) and suggested that such behavior seemed to have significance in facilitating mating activities in the first two groups. He pointed out that a

summit could represent a collecting point for a much larger area. Hudson (1905) found swarms of a coleopteran, *Pyronota* and *Bibio* (Bibionidae) as well as *Coccinella* on summits in New Zealand.

Van Dyke collected insects several times in the high Cascades and Sierra Nevadas and reported some of his observations in 1919. He found that high mountain snowbanks were good collecting areas for many insects which presumably had been carried there by winds, deposited on the snow and stranded because of inhibition of activity by cooling. He also noted many active insects and said, "About the bare peaks and ridges insects are also quite evident. Here, however, they are alive and active. Certain kinds even seem to have a particular liking for such localities, as for instance among the Diptera, the Bombyliidae, Syrphidae, and Tachinidae." Van Dyke also mentioned the presence of concentrations of ladybird beetles on high mountain peaks and ridges. Balduf (1935) cites many records of coccinellid aggregations at such points in various parts of the world. Gatherings of these beetles appear to be associated with hibernation. No mating or feeding activity seems to occur.

Several records of the presence of male horse botflies on rocky summits in Scotland are given by Walton (1930) who felt that summits might well represent mating sites for these flies. Townsend (1935) reported that males of *Cephenemyia* frequent high mountain tops at altitudes of 6,000 to 12,000 feet. Moreover he stated that in various other flies the males showed preference for definite localities or areas where they could be taken in numbers without any capture of females. Observations on summit-frequenting behavior of males of the horsefly *Tabanus sudeticus* recorded by Brauer are cited by Edwards, Oldroyd and Smart (1939). Widespread swarming of winged ants on mountain and ridge tops in the western United States is reported and discussed by Chapman. The distribution of sarcophagids and certain other flies on Georgia mountain summits has been studied by Dodge and Seago who used both net and trap sampling methods. These investigators took many species of flies by net far more commonly on the summits than elsewhere and found that a very high percentage of males was represented in summit net collections.

There is little doubt that air currents can carry insects upwards for considerable distances above the land surface. The study of airborne insect populations by Glick (1939) and others has revealed that even under ordinary atmospheric conditions many insects are carried aloft in this way. Some of the observations by Van Dyke and the report by Howard (1918) indicate considerable transportation of insects, at least at times, from lower altitudes up to higher mountain areas. Updraft currents undoubtedy originate when the mountain surfaces are heated, particularly during the summer days, and one would expect bare rocky areas to be especially productive of such currents.

Unfortunately such wind measurements as were made on Squaw Peak were not suitable for evaluation of extent or magnitude of updrafts. Their presence was indicated by the fact that on certain days cloud masses formed and hung above the peak and above visible mountain ranges some distance away but not over intervening areas. Also, on at least three separate occasions butterflies seen some 15 to 20 feet above the summit would suddenly start going upwards rather rapidly until out of sight. Nothwithstanding these and other indications of updrafts and their possible role in transporting insects to mountain peaks it is felt that the relative abundance of many of the insects found at the summit of Squaw Peak is not to be accounted for by wind or updrafts alone. There are several reasons for this view.

It is considered unlikely that updraft air currents are so symmetrical as to concentrate insects more at the very top of the peak than at the other relatively near and only slightly lower stations. Eddy currents would be expected to occur along the approaches to the summit and to thus result in some deposition of airborne insects there, particularly in view of the fact that there was general and almost constant wind from the southwest during most of the study periods. The greater numbers of smaller insects taken by the water pans at station A, as compared with those from the lower stations may well be explained by the occurrence of some vegetation at the summit. Pan data on the grasshoppers, which were all of flightless species and therefore not influenced much by updraft air currents, support this explanation. Also, updraft air currents, if a factor in transporting insects, might be expected to carry them on up above and away from the peak. In this connection, however, it may be pointed out that most of the insect activity occurs within the microclimate region (within about six feet of the surface). Insects already within this region would not be much affected by higher updrafts and this relatively quiet zone might provide an opportunity for insects to make contact with the surface.

It is very unlikely that updraft air currents would be so selective with respect to insect species or sex as is indicated by the observations and

other data, although differences in activity and distribution of insects prior to any influence by such currents would enter the picture. Also, air currents could hardly account for the continued presence of the large strong and fast fliers as *Cephenemyia,* the siricids, tabanids, tachinids and many syrphids and others which could easily leave the peak for lower elevations at almost any time regardless of wind velocity. Further, early-morning summit activity was frequently considerable by 8:00 a.m. when updraft currents would be expected to be slight if present at all.

On the basis of this study and the observations of others it is concluded that many insects, particularly the males, tend actively to seek and remain at hill and mountain summits. It would seem that in some of the Diptera and perhaps, judging from the Squaw Peak observations and collections, in certain families of the Hymenoptera, a tendency of the males to select "waiting stations" is correlated with a tendency to select prominent features of the landscape as such points. It is suggested that these insects are instinctively attracted to such points because they are conspicuous isolated topographic features and that visual reflex mechanisms are involved in the movement of such insects to these areas. It is not implied however that updraft air currents do not account for the presence of many insects at such points, particularly small weak flying forms, or that the complex of environmental factors associated with bare exposed rocky areas during summer months plays no role in causing summit insect abundance. The suggestion of Poulton's, mentioned previously, that mating would be facilitated by such an instinctive behavior pattern seems logical as a basis for attempting to explain its significance, and the fact that parasitic and not usually abundant groups of insects were well represented at the summit of Squaw Peak supports this idea. Additional and more intensive work is needed in order to describe and explain this phenomenon more adequately.

Summary

Studies were made during the summer of 1952 on insect populations at and near the summit of a 7,996 foot mountain in western Montana. Insects were sampled by bait fly traps, by oil-water pan traps and by net and the distribution of many insects about the summit was carefully observed. Activity levels at and near the summit were determined by counting auditory evidences of insect flight. It is concluded that certain species from several families of Diptera and some families of Hymenoptera are more abundant at the actual summit than at nearby lower areas. Considerable evidence indicates that such a distribution in these species cannot be attributed to the action of updraft air currents alone. It is suggested that an inherent tendency to seek prominent topographic features such as mountain summits is one of the bases of the phenomenon.

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SARCOPHAGIDAE AND OTHER DIPTERA TAKEN BY TRAP AND NET ON GEORGIA MOUNTAIN SUMMITS IN 1952

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INTRODUCTION

Most of the species of flies which commonly enter houses or restaurants and therefore are possible vectors of disease are attracted to baits composed of entrails, garbage, or feces. These flies can usually be collected by placing fly traps over such baits. Rather detailed population studies have been made of many of these common, saprophagous species. On the other hand, the writers noticed that certain museum collections contained very interesting, uncommon, or undescribed species of muscoid flies, principally Sarcophagidae, and that many of these specimens bore a mountain locality label. The writers, therefore, chose nearby Stone Mountain as a site for operating fly traps to determine if these rarer species could be collected in this manner. Thirty-four trap collections were made about the base and upon the sides of the mountain from April 14 to May 31, 1952. These collections yielded over 21,000 flies, of which nearly 1,100 were sarcophagids and only 11 males and 20 females were considered to represent uncommon species. On May 2, while one of the writers set traps the other climbed to the summit of Stone Mountain and in a 60-minute period collected 31 sarcophagids, of which 29 were males of uncommon species. This is equivalent to 29 specimens of uncommon species per man-hour, compared with 0.076 such flies per trap-hour. Another expression is that 85 percent of the netted flies and only 0.14 percent of the trapped flies were unusual sarcophagids.

With this initial discovery, trapping in the vicinity of the mountain was abandoned, and the summit of Stone Mountain was visited 13 times in May and June. Other summits were also visited on one or more occasions, beginning with the following dates: Kennesaw Mountain, June 12; Rabun Bald, June 20; and Mount Enotah, July 13. In addition, seven other summits in northern Georgia were visited a total of nine times during July and August.

By late June, collecting at Stone and Kennesaw Mountains had become unprofitable, probably due to extreme drought conditions, so there are practically no records from these mountains during July and August. In the environs of Rabun Bald and Mt. Enotah, some rainfall occurred, and collecting was concentrated there during this period. In the fall, collecting was continued on Stone and Kennesaw Mountains, Rabun Bald, and Mount Enotah, at two to four week intervals until the last week of October.

Prior to late June, traps were set out overnight, but often most of the collections were destroyed by ants, the baits were stolen by mammals, or the traps were otherwise disturbed. By early July, it was decided to make trap collections during the same period that net collections were made. It was extremely useful, for purpose of comparing and evaluating the results of the two modes of sampling fly populations, to have the collection periods coincide.

This paper contains a comparison of the collections made by net and by baited trap on mountain tops in Georgia during 1952. Collecting was continued in the spring of 1953 to complete records for a full year. This paper is considered to be a preliminary report, since the 1953 data have not been tabulated and indentifications of the 1952 specimens have not been completed. A final report awaits the completion of this work and the description of the new species.

METHOD OF COLLECTING

The traps employed were of the usual fly trap construction, 9 inches in diameter and 12 inches high (Fig. 1). Each trap was set over a bait which usually was chicken entrails but occasionally was human feces. In addition, several collections made by net over feces were grouped with the trap collections. Only the collections from traps set on summits were taken into account in the statistical analysis that follows.

Net collections were made by an ordinary insect net, preferably one with a bag of 10 inches diameter or less. Flies were collected as they were observed resting upon the ground, rocks, logs, vegetation, or upon the surface of forestry observation towers. Little attention was given to flies frequenting flowers, and practically no sweeping was done. A few flies were taken while hovering in the air, especially in the late fall when other collecting was not fruitful. In general, net collecting was very selective. The great majority

FIG. 1. Collecting apparatus. Fly traps with aerosol bomb for killing flies and a carboard carton for storing trapped flies. The trap is made from a 2½ gallon cardboard ice cream carton, with a 16-inch-mesh screen cone and a 2-inch strip of half-inch hardware cloth soldered to the wire bead on its base. A piece of transparent plastic is secured over the top by an elastic band. Besides the net are a chloroform tube and several boxes for temporary storage of the netted flies.

FIG. 2. Observation tower at Rabun Bald. Collecting sites shown here are the ground and rocks at the base of the tower, the sides of the tower, the catwalk, and the utility pole in the left background. One species was collected only on or near the utility pole, another only on the underside of the catwalk. Upon the catwalk most flies rested on the handrail, or upon the outer edge of the walk. Flies were observed to rest upon the chimney and aerial, but could not be collected.

of the flies were secured by stalking individual specimens when they were seen resting upon some surface, and, where a choice existed, sarcophagids were collected in preference to flies of other families. No net collections were made within 7 feet of a trap. Fur further details of the collecting apparatus, see Figure 1.

DESCRIPTION OF THE MOUNTAINS

Stone Mountain, De Kalb County, is a granite outcropping 1,686 feet in altitude and about 650 feet higher than the surrounding countryside. Some shallow patches of soil on its sides are sodded, and some pines and cedars grow upon its sides. The summit is bare rock and is moderately level.

Kennesaw Mountain, Cobb County, is comparable in size to Stone Mountain, but over 1,800 feet in altitude and is forested to the summit, which is a ridge about 150 feet long with sparse vegetation and rock outcroppings. Both ends of the ridge are forested (Fig. 4).

Rabun Bald, Rabun County, in the northeast corner of Georgia, is 4,714 feet high and is the highest mountain in the vicinity. The sides are forested up to a grassy summit about 150 feet in diameter (Fig. 2).

Mount Enotah, or Brasstown Bald as it is more commonly known, is the highest point in Georgia, with an elevation of 4,782 feet (Fig. 3). It is located on the Towns and Union County line. Its slopes, too, are forested, but the grassy and bushy summit is somewhat larger than that of Rabun Bald.

FIG. 3. Summit of Mount Enotah, showing the base of the tower, a metal tool shed (extreme right), a metal storage bin for firewood (left), and some bushes (background, center) on the northern edge of the bald. Most flies were collected from the bushes, the ground, the storage bin or tool house, or the lower two horizontal braces of the tower. Some were also taken from a picnic table and woodpile, which are not shown.

FIG. 4. Kennesaw Mountain, path and woods at south end of the summit. More flies were taken in the wooded ends of the summit than upon the open summit itself, in contrast to the results obtained on the other summits.

The other mountains visited in 1952 were not as productive as the four named above. This was due, perhaps, to physical features of the summit or to the season at which they were visited. Furthermore, access to their summits often was more difficult. For these reasons, collecting was concentrated upon the four mountains described above. All four are the highest points in their respective vicinities, and all have forestry observation towers or similar structures on their summits.

RESULTS

A. *Trap and Net Captures of Muscoid Flies*

Table I summarizes results of all trap and net collections on the four principal summits and of the four principal muscoid families. Attention is called to the percentage column at the extreme right. Ninety-five percent of all trapped flies are of the first three families listed. The net collections display a greater percentage of sarcophagids, larvaevorids, and miscellaneous other families, but a much lower percentage of calliphorids and muscids.

Table II compares the total Diptera and total sarcophagids taken per hour by trap and by net for certain outstanding collections and for the season. The maximum number of sarcophagids per hour was 152.3 by trap and 56.6 by net, compared with season averages of 29.8 and 21.4 respectively. The trap and net figures for Rabun Bald on August 12 are of especial interest. A great decline in the abundance of the saprophagous species is indicated by the trap collections, whereas the net collections took maximal numbers of sarcophagids and total flies.

In Table III, the sex ratio of the collected flies is illustrated only for certain sarcophagids. For convenience, all species are divided into two groups. Group A includes those species that have been reared from excrement, dead animal matter, or garbage, or are known to be commonly attracted to fly trap baits, and, therefore, may be assumed to be saprophagous. *Ravinia querula* (Wlk.) is remarkable in that it is common to both trap and net collections with an average sex ratio of nine males per female. Two other saprophagous species, *Ravinia ochracea* (Ald.) and *Sarcophaga crassipalpis* (Macq.), were locally common as males in net collections. The male : female sex ratio for these three species is 14 :1 in net collections and nearly 7 :1 in total collections. *Oxysarcodexia ventricosa* (Wulp) was by far the most common species, representing nearly 43 percent of all sarcophagids collected. Over 99 percent of all *O. ventricosa* were trapped and in a ratio of nearly five females per male.

Group B of Table III include species which are

TABLE I. *Summary of total diptera and four principal families by locality.*

	Stone Mt.	Kennesaw Mt.	Rabun Bald	Mount Enotah	Misc. Other	Total	% of Total
A. TRAP COLLECTIONS							
Sarcophagidae	828	2132	2359	688	1753	7760	37.5
Calliphoridae	1790	2130	923	589	298	5730	27.5
Muscidae	312	2609	1186	1043	1125	6275	30.0
Larvaevoridae	7	11	163	34	1	216	1.0
Other Families	132	112	231	327	28	830	4.0
TOTAL DIPTERA	3069	6994	4862	2681	3205	20811	100.0
No. Collections	10	10	15	12	8	55	
No. Trap Hours	67	43	72	55	23	260	
B. NET COLLECTIONS							
Sarcophagidae	355	859	1853	605	289	3961	59.4
Calliphoridae	0	26	54	84	19	183	3.2
Muscidae	9	48	190	174	23	444	6.7
Larvaevoridae	78	246	477	161	27	989	14.6
Other Families	149	113	354	450	26	1092	16.1
TOTAL DIPTERA	591	1292	2928	1474	384	6669	100.0
No. Collections	16	10	11	7	9	53	
No. Net Hours	30	46	58	37	14	185	

TABLE II. *Total Diptera and Sarcophagidae, outstanding collections and per season.*

Method	Locality	Date	Hours	Diptera (total No.)	Sarcs (total No.)	Diptera (No. per hour)	Sarcs (No. per hour)
TRAP:	Levelland Mt.	July 13	1.33	484	196	363.0	147.0
	Blue Mt.	July 20	2.0	707	161	353.5	80.5
	Rabun Bald	July 4	6.0	1727	914	287.8	152.3
	Rabun Bald	Aug. 12	6.25	392	122	62.6	19.5
	TOTAL	SEASON	260.00	20,811	7,760	80.0	29.8
NET:	Levelland Mt.	July 13	1.165	69	66	59.1	56.6
	Rabun Bald	Aug. 12	6.5	516	360	79.4	55.4
	TOTAL	SEASON	185.0	6,669	3,961	36.0	21.4

TABLE III. *Further analysis of some Sarcophagidae by sexes.*

Species Taken	Trap		Net		Trap & net Male & female
	Male	Female	Male	Female	
A. SAPROPHAGOUS SPECIES					
Boettcheria latisterna Parker	2	0	41	11	54
Chaetoravinia derelicta (Wlk.)	100	316	2	2	420
Ch. latisetosa (Parker)	35	246	6	21	308
Helicobia rapax (Wlk.)	34	61	24	16	135
Oxysarcodexia cingarus (Ald.)	9	43	0	1	53
Ox. galeata (Ald.)	26	178	1	1	206
Ox. ventricosa (Wulp)	868	4,107	5	32	5,012
Ravinia pusiola (Wulp)	283	59	25	2	369
R. ochracea (Ald.)	126	87	184	8	405
R. querula (Wlk.)	257	44	674	53	1,028
Sarcophaga bullata Parker	149	136	7	4	296
S. crassipalpis Macq.	7	2	66	2	77
S. nearctica Parker	48	26	31	4	109
S. sarracenioides Ald.	3	7	1	0	11
S. utilis Ald.	175	46	4	2	227
Others	17	60	11	3	91
TOTAL	2,139	5,418	1,082	162	8,801
B. PARASITIC SPECIES					
Spirobolomyia basalis (Wlk.)	10	21	484	7	522
Sarcophaga "*sima* group," 14 spp.	13	10	1,045	17	1,085
Acanthodotheca (*s. lat.*), 8 spp.	10	11	316	11	348
Orthopterous parasites, 5 spp.	1	0	79	2	82
Sarcophaga fulvipes Macq.	18	3	75	2	98
S. offecta Lopes	61	10	83	1	155
Laccoprosopa sarcophagina Tns.	10	1	240	10	261
Macronichia aurata (Coq.)	0	1	94	159	254
Emblemasoma erro Ald.	0	0	3	0	3
Johnsonia spp.	0	0	0	2	2
Miltogramminae	0	4	27	7	38
Others	8	11	42	11	72
TOTAL	131	72	2,488	229	2,920
TOTAL—ALL SARCOPHAGIDAE	2,270	5,490	3,570	391	11,721

known or assumed to be parasitic in the larval stage. The first four listings include 28 species which display large numbers of males in the net collections. It is of particular interest to note that 94.4 percent of all specimens collected were netted males. The preponderance of netted males continues throughout Table III B with one notable exception. Females of *Macronichia aurata* (Coq.) account for 69.4 percent of all netted females of the parasitic species. The table does not show that the male: female ratio for this species is 26:118 from Mount Enotah but is 63:14 from Rabun Bald. The reason for this disparity in the sex ratio is not evident.

The evidence of parasitism of many of the species in Table III B is indirect, for nothing is known of their habits except that they have not been saprophagously reared and that they are not strongly attracted to the usual fly trap baits. However, there is definite evidence of parasitism in many cases. Unpublished records indicate that two species of the *Sarcophaga sima* group are parasitic upon snails and the katydid, *Pterophylla camellifolia* (Fab.), and a third is very closely related to a species which has been reared from *Curculio* larvae. Species of the genus *Acanthodotheca* have been reared from adult beetles, especially Scarabaeidae. *Macronichia* are parasitic on Hymenoptera; the females have an elongated, awl-shaped larvipositor adapted for inserting their maggots directly within the host. *Sarcophaga offecta* Lopes is closely related to two species which have been reared from *Polistes* nests in Texas and Argentina. *Spirobolomyia basalis* (Wlk.) is closely related to two species which have been reared from millipedes of the genus *Spirobolus*. It is well known that the Miltogramminae breed in the nests of Hymenoptera.

Approximately 64 species of sarcophagids were collected by net, compared with 41 by traps. Thirty-four species were taken by net only, and about 15 of these apparently are new to science. The total number of species taken by both trap and net is about 75.

Table IV shows the composition of Calliphoridae in the collections. The majority of the species are rare or absent in the net collections. However, species of *Calliphora* were frequently observed on the summits and many were netted. Two species of *Protocalliphora* were taken by net only. The larvae of this genus are parasites of nestling birds.

TABLE IV. *Analysis of Calliphoridae.*

Species Taken	Trap	Net	Trap and net
Calliphora livida Hall	15	3	18
C. vicina R-D.	353	118	471
C. vomitoria (L.)	344	31	375
Callitroga macellaria (Fab.)	1,045	1	1,046
Cynomyopsis cadaverina (R-D.)	3	0	3
Lucilia illustris (Mg.)	14	0	14
Phaenicia caeruleiviridis (Mg.)	1,471	2	1,473
P. cluvia (Wlk.)	1	0	1
P. cuprina (Wd.)	2	0	2
P. sericata (Mg.)	162	0	162
Phormia regina (Mg.)	2,311	1	2,312
Pollenia rudis (Fab.)	9	0	9
Protocalliphora spp.	0	27	27
TOTAL	5,730	183	5,913

Table V shows the composition of Muscidae (including the Anthomyiinae) in the collections. Again, many of the species are rare or absent in the net collections. Only *Anthomyia, Coenosia, Orthellia caesarion* (Meigen), and *Hylemya cilicrura* (Rond.) were relatively common in the net collections. Among the undetermined species taken by net were many male Anthomyiinae which were unfamiliar to the writers and not commonly taken by trap. Undetermined species

TABLE V. *Analysis of Muscidae.*

Species Taken	Trap	Net	Trap and net
Anthcmyia spp.	37	58	95
Coenosia spp.	4	30	34
Dendrophacnia spp.	0	6	6
Fannia americana Mall.	51	0	51
F. canicularis (L.)	36	0	36
F. curvipes Mall.	9	0	9
F. difficilis (Stein)	971	3	974
F. enotahensis Seago	54	0	54
F. femoralis (Stein)	5	0	5
F. howardi Mall.	16	0	16
F. manicata (Mg.)	15	2	17
F. pellucida (Stein)	55	0	55
F. pusio group females	315	0	315
F. scalaris (Fab.)	77	0	77
Fannia spp.	169	6	175
Hebecnema umbratica (Mg.)	5	0	5
Hydrotaea houghi Mall.	605	1	606
H. occulta (Mg.)	23	0	23
Hydrotaea spp.	20	4	24
Hylemya cilicrura (Rond.)	85	39	124
Limnophora arcuata Stein	1,139	0	1,139
L. cilifera Mall.	5	0	5
Morellia micans (Macq.)	157	9	166
Musca domestica L.	111	4	115
Muscina assimilis (Fall.)	244	2	246
M. aurantiaca Hough	86	4	90
M. stabulans (Fall.)	6	1	7
Myiospila meditabunda (Fab.)	86	10	96
Ophyra leucostoma (Wied.)	621	0	621
Orthellia caesarion (Mg.)	16	26	42
Paregle cinerella (Fall.)	90	4	94
Pyrellia cyanicolor (Zett.)	987	17	1,004
Scopeuma furcatum (Say)	3	0	3
S. stercorarium (L.)	2	2	4
Stomcys calcitrans (L.)	0	2	2
Synthesiomyia nudiseta (Wulp)	5	0	5
Undet. spp.	165	214	379
TOTAL	6,275	444	6,719

represented 48.2 percent of the netted muscids and only 2.6 percent of the trapped muscids.

B. *Occurrence of Netted Flies on the Summits*

It was first noticed at Stone Mountain that *Sarcophaga sima* Aldrich was taken on the observation tower but not on the rocks at the base of the tower. Then at nearby Kennesaw Mountain it was found that the five species most common at Stone Mountain were rare or absent in net collections, or were taken on low vegetation or rocks in the woods at either end of the summit, and not upon the exposed summit itself. *S. offecta,* the second most abundant species at Stone Mountain, was never netted at Kennesaw Mountain, but was found sparingly in traps at both summits. Many species taken at Kennesaw Mountain were not seen at Stone Mountain.

Rabun Bald was the most interesting summit because it provided the widest variety of collecting sites. It was found that *S. basalis* was particularly abundant on projecting rock ledges and *R. querula* on the ground or rocks at the base of the tower. Certain species were found on the stone foundation of the tower, some on the shaded and others on the sunny side. Some species were found primarily upon the catwalk of the tower about 15 feet above the ground, others were most common upon the foliage at the northwestern margin of the bald opposite the sun. Very few flies were found on the southeastern margin of the bald, but a tiny shelter house in this vicinity had its characteristic species. Nearly all specimens of *Protocalliphora* were taken from a utility pole 15 feet from the tower. None were ever observed upon the tower itself. Some flies were observed to alight repeatedly upon the trunks and larger limbs of the scrub oaks which fringed the bald, but could not be netted because of the protection afforded by the smaller branches.

Thus it was established rather early during the net collections that many species had definite resting preferences, rather than being found scattered indiscriminately on the various resting stations that each summit provided. However, the preferred station for a given species may differ greatly from summit to summit. For example, it has already been observed that *S. basalis* was especially abundant on projecting rock ledges at Rabun Bald. These ledges were horizontal and faced to the west. At Kennesaw Mountain this species was taken principally upon an upright stone about 4 feet high near the southern end of the summit, and at Levelland Mountain it was common on a prostrate log which received direct sunlight in a wooded area. At Stone Mountain, *S. basalis* was never netted on the summit, although it was both trapped and netted at the base of the mountain. Is it possible that this species visited the summit of Stone Mountain but found no suitable resting station, and hence was never netted? The particularly barren nature of the summit of Stone Mountain is in contrast to the other mountains studied.

The barren nature of Stone Mountain may also account for the fact that all but two of the netted males of *S. offecta* were taken on this mountain although the trap records demonstrated its presence on four of the other eight summits. Perhaps on the other summits this species takes station in the tree tops and thus escaped the collector's nets.

The abundance of the flies varies with the hour of the day. Early morning collecting on Stone Mountain where resting flies have minimum cover and thus should be easily observed has yielded no Diptera until 7:30 a.m. The first flies to arrive were larvaevorids, and the first sarcophagids were seen at 8:00 a.m. At Mount Enotah, early morning collecting yielded only species of *Calli-*

phora, the first sarcophagid being found at 7:15 a.m. The best hours of collecting are from 9:00 a.m. until noon, though some interesting captures were made much later in the day. In general, afternoon collecting yielded fewer flies per hour and a larger proportion of saprophagous sarcophagids. At Kennesaw Mountain, June 15, the sarcophagid parasite: saprophage ratio was 93:46 in the morning (10:20 a.m. to 12:00 m.) and 52:64 in the afternoon (12:40-2:40 p.m.). On June 27 collecting at Kennesaw Mountain was discontinued at noon because after 11:00 a.m. collecting was poor and limited primarily to a saprophage, *R. ochracea.*

The abundance of flies upon a summit as expressed by net collecting is not in direct proportion to its height or mass. Collecting was more productive at Rabun Bald that at Mount Enotah and at Kennesaw Mountain than at Stone Mountain, although Rabun Bald is approximately equal to Mount Enotah, and Kennesaw Mountain is approximately equal to Stone Mountain.

When the weather was unfavorable, collecting was poor, as may be expected. Collecting in cold, rainy, or extremely windy weather yielded negative results. However, fly activity was noted during moderate to strong winds, and flies soon reappeared after light rains if the sun came out. Flies were active, and the temperature surprisingly warm, on Rabun Bald at 9:15 a.m., October 25, though frost from the previous night was still present in the valleys. In intermittent sun there was a marked increase in fly activity with the advent of the sun.

C. *Observations on Mating*

In 185 hours of summit collecting the writers observed only 21 mated pairs of muscoid flies, of which 19 were sarcophagids and 2 were larvaevorids. In no instance was the beginning or the normal temination of the act of copulation observed. The majority of mated pairs were observed during the late morning hours which were also the average time at which collecting was performed. Mated pairs of sarcophagids were often as difficult to capture as single specimens, at times taking flight before the collector came within range.

The behavior of two pairs of sarcophagids at Stone Mountain was noteworthy. These were large-bodied species, possibly *S. hamata* Ald. or *affecta.* One pair, when alarmed, tacked into a brisk wind at about a 45° angle and flew out of sight, maintaining a level course, or possibly following the gentle contour of the mountain summit. Due to their large size and to their flight being slowed by the wind, it was possible to watch their progress in flight for several seconds. Another pair, on a very windy day, was extremely wary and never allowed the collector to come within range; after taking flight six to eight times they became lost from sight. It is difficult to believe that under these circumstances only the female took flight, or that the male was less aware of external stimuli. With regard to mismatings, or pseudo-copulation, it is not believed that any of the 15 captured pairs were mismated, and only once did a captured pair prove to be two males of the same species.

The writers did not recognize courtship as such, and initiation of copulation was not observed. However, certain flights which might have been interpreted as courtship were often observed. These were apparently playful pursuit of two or more males when one alighted on or flew near another. One pursued another as it flew nearby, or if one alighted near another, both quickly took wing, and a short time later one or both alighted upon the original site, which was likely to be the highest point of a stone or a certain leaf of a shrub.

On another occasion (Stoughton, Wis., August 1952) one of the writers observed flies of a species of the sarcaphagid genus *Camptops,* resting on tree trunks, to attack each other repeatedly, one alighting momentarily upon another, whereupon they both would take wing. This might have been interpreted as brief copulation, such as may occur in *Musca* (Hammer 1942) except that all of the 80 specimens captured proved to be males. *Camptops* was not represented in the Georgia summit collections, and its peculiar behavior indicates the danger of generalizing on the habits of a group of insects from observations made upon only a few species within that group. Certain aspects of mating behavior described by Thomas and by Hammer (see Discussion which follows) are beyond the writer's comprehension, yet may actually be normal to the species studied.

An interesting capture in southern Georgia by R. E. Bellamy was a mated pair of *Chaetoravinia derelicta* (Walker) by a light trap. The couple was joined together in death. It seems possible, though improbable, that the couple met at night in the vinicity of the light. It is more likely that diurnal copulation was not completed by nightfall, and that upon being disturbed the couple flew to the light. Whichever is the case, this record is most unusual in view of what is known or assumed of the diurnal habits of muscoid flies. *C. derelicta* is not commonly netted on mountain summits.

To return to the sarcophagid and larvaevorid male populations observed on summits, very few apparently have the opportunity to mate in such situations due to the scarcity of females. However, with certain species, the only netted females have been taken in copulation. Of two common species, *R. querula* and *M. aurata,* only one mated pair of each was taken in a total of 1,282 males and females collected by net. The netted females of these species were 53 and 159 respectively. Forty-four additional females of *R. querula* were taken by trap while net collections were being made. With this total population of females upon the summits, the collection of ony two pairs in copulation appears to be unusually low and quite insufficient evidence to justify summit-frequenting habits of these two species for the purpose of copulation. *Fabriciella florum* (Wlk.) was another common summit-frequenting species in which copulation was not observed.

Other Diptera observed mating on summits were the syrphid, *Tubifera tenax* (L.), one pair; the tabanid, *Tabanus reinwardti* Wd., one pair; the bombyliid, *Villa sinuosa* (Wd.), one pair; and the phorid, *Beckerina orphnephiloides* Malloch, numerous pairs. The latter were common on Mt. Enotah, October 25, on the shaded side of a metal building at the base of the tower. Most females were quickly attended by one or more males as soon as they appeared. Males predominated in the sample captured: 146 males, 55 females.

The complete lack of observations of copulation in the Muscidae, Calliphoridae, and some common saprophagous species of Sarcophagidae, may be due in part to the fact that most specimens were attracted directly to the traps and no net collecting was done within 7 to 15 feet of a trap.

Discussion

Chapman (1954) has reviewed the literature on summit behavior of insects in general. The writers repeat several references of special interest to this study and add others.

Aldrich (1931) lists *Sarcophaga thatuna* Aldrich as being taken only from the summit of Moscow Mountain, Idaho.

Aldrich (1915) translated several accounts from Brauer (1863) or bot fly summit-frequenting behavior and described a new species from Mount Washington, N. H.

Alexander (1940) gave a very detailed entomological account of Mount Washington, N. H. and environs, with metereological data. The climate at the summit is severe, and apparently only occasional days are favorable for voluntary insect flight. It was pointed out that the white sides of a building located at the summit attracted many insects.

Townsend (1935) expressed the theory that male muscoid flies of certain species take station where they await the female. This is not elaborated in detail, but is most clearly set forth in paragraph 4, page 184. Three other remarks, on pages 217, 222, and 226, refer to the male-station habit in bot flies. He stated, in effect, that males of many species whose larvae are parasitic upon warm-blooded animals or in which the adults are blood-sucking, will take station high upon tree trunks, on hill or mountain summits, or upon other situations, where they await the females.

Thomas (1949, 1950) referred to the male station-taking habit of certain Oriental species of Sarcophagids. In the first paper, four new species were described from a series of males taken on a mountainside, on rocks near a hot spring, or on pine trees on a mountain summit. With regard to resting preferences he stated in the second paper "so constant were these habits that one could be almost certain of collecting a given species in the locality indicated here."

Weiss (1927, 1928) recorded 17 sarcophagids of a total of 105 Diptera taken on forestry lookout towers in New Jersey. The second ranking family was Tipulidae. The figures were very small for 2-year records (1926 and 1927) from six or more towers.

Felt and Chamberlain (1935) listed over a thousand species of insects taken at some height in the air in New York State, the majority of their specimens having been taken from the roof of the State Education Building in Albany, at an elevation of 128 to 148 feet above street level. Most of the insects were collected from the gutters to which they were blown after being killed or disabled by alighting upon the hot metal of the roof. They recorded 130 specimens of sarcophagids of 11 species. These include 34 specimens taken from two forestry lookout towers and nine undetermined specimens taken from the roof of a 30-story building in New York City. In the Diptera, sarcophagids were exceeded in numbers only by calliphorids and muscids (including anthomyiids), due to the abundance of the two species, *Pollenia rudis* (Fabr.) and *Muscina pascuorum* (Meig.). Both of these species occur in Georgia, but were rare or absent in summit collections.

Glick (1939) reported upon insects taken by airplane for a 5 year period at Tallulah, La. Of a total of 28,514 insects only 31 specimens were sarcophagids, which were taken only during daylight hours and at altitudes of 20 to 5,000 feet. This is a very detailed paper of great importance

for a better understanding of flight habits of many diverse groups of insects.

Timon-David (1937) studied the high mountain Diptera of Mont Blanc in the French-Italian Alps and in an adjacent valley. Syrphids predominated in the collections at the lower stations and anthomyiids at the higher levels. Important references are given, including one by Bezzi on the Italian Alps.

Walton (1930) summarized the summit-frequenting behavior of *Gasterophilus intestinalis* DeGeer in Great Britain. Males of this species have been taken on many occasions on high rock outcroppings far from domestic horses. On only one occasion was a female observed; three males pursued her and all four fell to the ground. Walton comments upon the rarity of males about domestic horses, and raises the question "do the males assemble on hilltops or in the upper air to be there sought out by the females?"

Hammer (1942) mentioned the peculiar habit of oestrids meetings over the highest point in the field, or even over mountain peaks, for the purpose of mating.

Swan (in a private communication, December 28, 1952) suggested an inverted-funnel theory to explain insect accumulations on mountain tops, adding that under particular conditions many insects may voluntarily fly up the sides of the "funnel" to the summit. This behavior is quite separate from the involuntary drifting of many insects by convection currents or storms, with resultant accumulation of insects such as have been reported on snowbanks at high altitudes.

The mating of sarcophagid flies was described in detail by Thomas (1950) for several Oriental coprophagous species. He stated that copulation usually took place near a food supply and that the males selected their mates by a process of trial and error, often attempting to couple with other males or with females of other species or even of other families before a suitable mate is found. Copulation was of long duration, lasting at least 4 hours in one instance, and when a mated pair was disturbed the female took wing, except occasionally when the male was the larger of the two. The position was the usual one assumed by muscoid flies, the male mounting the female and both facing the same direction. Copulation was most frequently observed during the heat of the day.

Hammer (1942) described the mating of many species of Danish coprophagous flies. The only sarcophagid in his account is *Ravinia pernix* (Harris), there recorded as *Sarcophaga striata* (Fab.). Of this species and certain others, he merely stated that the couples pursue each other into the air before tumbling to the ground.

In the references cited there is an indication of abundance of sarcophagids on summits by Felt and Chamberlain (1935), Weiss (1927, 1928), and Chapman (1954). Indication of capture of rare species on summits is made by Aldrich (1915, 1931), Chapman (1954), Felt and Chamberlain (1935), Thomas (1949) and Timon-David (1937). The studies by Chapman (1954), Walton (1930) and Townsend (1935) indicate that males predominated in the samples captured. The lack of any reference to muscoid flies in the detailed account by Alexander (1940) is likely due to other interests of the author and of the collectors from whose material information was gathered.

Evidently the present article is the first which indicates the results of intensive summit net collecting of muscoid flies. Chapman (1954) did relatively little net collecting since he relied also upon activity counts and upon two types of traps to furnish data on summit insect populations. Timon-David (1937) and Bezzi, to whom he referred, found anthomyiids predominant and sarcophagids scarce in the European Alps, evidently because they collected in alpine meadows and not from summits.

Chapman (1954) showed that insect activity was much greater at a summit than at several points only slightly removed from it. The writers' observations confirm this.

The maximum and minimum altitudes at which a summit is favorable for unusual insect activity have not been determined. The Georgia mountains investigated vary from 1,650 to 4,780 feet in altitude. Glick (1939) reported insect activity at the summit of Long's Peak, Colo., at an elevation of 14,255 feet. The maximum heights to which insects fly is probably dependent upon favorable temperatures and other weather conditions, and would be expected to be greater in the tropics than in temperate or arctic regions.

It is evident from the original data given and from the references just cited that many insects occur on summits in unusual abundance. In many instances this cannot be explained by aerial drift caused by convection currents or storms. Their accumulation upon such sites apparently does not fulfill any important biological function, other than copulation, which has been observed only rarely. The presence of many species of insects on summits may be an evidence of normal dispersion by flights to the upper air, but this explanation is untenable when virtually no females of a species are represented in the samples collected. This

is particularly true of the muscoid flies reported herein.

A number of stimulating questions have arisen:

1. From how far are these males attracted to a summit?

2. Assuming that the flies breed elsewhere and do not remain upon the summit overnight, do they return to the same locality nightly?

3. Do males of these species congregate elsewhere where there is no local vertical prominence? If so, where?

4. What are the life histories, female habits, and usual sex ratios of these species?

5. Assuming that this summit phenomenon is an important part of their mating behavior, are any species restricted to a mountainous environment?

6. What species occur on the tops of the tallest office buildings in downtown Atlanta?

7. Do the flies fly up the sides of the mountain, or are they attracted to a summit from a great distance while flying in the upper air?

8. How many additional species live in the environs but do not visit the summits of the mountains?

9. To what extent is the composition of net collections influenced by the particular interest of the collector?

Summary

Fly traps set upon mountain summits yielded the usual composition of saprophagous muscoid flies, and in the same sex ratio for the various species that one would expect of traps set elsewhere in the vicinity. Three muscoid families, Muscidae, Calliphoridae, and Sarcophagidae, occurred in approximately equal proportions, and with a high percentage of females of saprophagous species.

There was a marked difference in the composition of trap and net collections except for an occasional species common to both. Many saprophagous species were rarely taken by net even when flies were netted 7 to 15 feet from a trap.

In net collections, many species of flies, both parasitic and saprophagous in nature, occurred commonly on summits and usually as a very high percentage of males. Observation of 21 mated pairs of muscoid flies would seem to substantiate Townsend's theory that males take station on summits to await the female, but this evidence is not conclusive. Many undescribed species (principally in the *Sarcophaga sima* group and the genus *Acanthodotheca* in the broad sense) or little-known species were taken in the net collections. The females and life histories of most of these species are unknown.

The writers's observations confirm those of Chapman that many insects, especially Diptera, occur commonly and are very active upon mountain summits during favorable weather, that they are much more abundant at the summits than at even a short distance below the summits, and that they occur as a very high proportion of males in the samples of Diptera which were collected.

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The identified diptera mentioned in this paper were identified by the writers, with the following exceptions: Tabanidae, Graham Heid; Phoridae, George C. Steyskal; Bombyliidae, W. W. Wirth.

The writers are particularly indebted to Professor P. W. Fattig of Emory University, Ga., who, in effect, prompted this study. In material which he placed at our disposal there were a number of species of Sarcophagidae which have been rarely, if ever, taken by baited trap. The majority of these specimens bore a mountain locality label.

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FORAGE PRODUCTION ON LONGLEAF PINE LANDS OF SOUTHERN ALABAMA

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Forest lands are a very important source of grazing for cattle in southern Alabama, but the proper coordination of cattle grazing with timber-growing requires information on forage growth under various forest conditions. This paper reports the initial results of a study of forage production as influenced by timber stand, tree litter, forest types, and soils on the Escambia Experimental Forest, near Brewton, Alabama. The application of these results is mainly in terms of grazing capacity and forest range management.

Experimental Area

Of the 3,000 acres that comprise the Escambia Experimental Forest, 60 per cent is second-growth longleaf pine (*Pinus palustris* Mill.), 15 per cent is upland scrub oak, and 15 per cent is hardwoods, brush, and slash pine (*P. elliottii* Engelm.) along creek bottoms.

The herbaceous growth, even within a limited area, varies greatly in both kind and amount, owing to the patchiness of the timber stands, the rolling topography, and the intermingling of very different soil types. In the uplands, the principal grasses are little and slender bluestems (*Andropogon scoparius* Michx. and *A. tener* (Nees) Kunth), Indian grass (*Sorghastrum nutans* (L.) Nash), blue dropseed (*Sporobolus junceus* (Michx.) Kunth), and species of *Panicum, Aristida,* and *Muhlenbergia.* The most important forbs are *Chrysopsis graminifolia* (Michx.) Nutt. and swamp sunflower (*Helianthus annuus* L.). Gallberry (*Ilex glabra* (L.) Gray) is the predominant shrub.

Along the creek bottoms, the predominant understory species are switch cane (*Arundinaria* sp.), *Muhlenbergia* spp., *Panicum* spp., sedges (*Carex* spp.), beakrushes (*Rhynchospora* spp.), gallberry, and waxmyrtle (*Myrica* sp.).

Study Methods

Production of grasses and forbs was inventoried in November, 1948, on 24 well-distributed compartments, each 40 acres in size. Plots were 9.6 square feet in area, and were located systematically with 5, 10, or 20 plots per compartment. The herbage was clipped and weighed in accordance with the procedure described by Campbell and Cassady (1949). The analysis of herbage production is based on 141 unburned plots in the uplands and 26 in the creek-bottom type. The plots were very lightly grazed.

Timber stand was computed in terms of basal area per acre for all trees 4.5 feet or more in height on a circular plot 16.65 feet in radius (0.02 acre), with the square herbage plot at the center.

Tree litter was measured by gathering and weighing the pine needles and hardwood leaves on each square herbage plot. The litter was mainly the accumulation from previous years, since it was measured in November before most of the 1948 leaf-fall occurred.

Upland soils were classified on each plot from a boring made to the depth of 30 inches.

Upland Timber Stands

The relationship of grass and forb production to basal area of the timber stand in the upland forest types is graphed in Figure 1. Average herbage production decreased rapidly from about 1,000 pounds per acre at 0 basal area to about 700 pounds at 40 square feet of basal area. Above 40 square feet, the herbage decreased less rapidly. It reached a low of about 475 pounds at 110 square

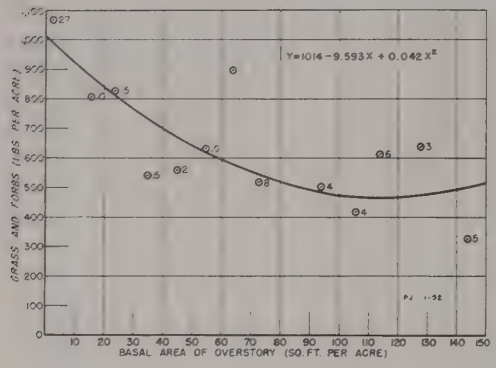

FIG. 1. Basal area of overstory competition and herbage production (air-dry) on upland sites. Number of observations in average are beside each datum point (two plots are beyond the abscissa of the chart).

feet of basal area per acre. The upturn in the curve (Figure 1) at this point may be artificial, in view of the limited data in the upper range of basal areas. However, it may also reflect a real upward trend of herbaceous production in older stands with higher basal area but fewer trees and more side light (Bond and Campbell 1951). The curvilinear regression accounts for 14 per cent of the variation in herbage production between plots in the uplands.

A special study indicated that much of the variation in herbage production is caused by differences in distribution of the tree stand, *i.e.*, whether the trees occur as isolated individuals or in groups. The grass cover was estimated on contiguous milacre plots along transects running from the trees into nearby open areas. For single longleaf pine trees 7 to 14 inches d.b.h., the zone of influence on grass cover extended out about 6 to 8 feet from the tree (Table I). For forest walls or groups of trees averaging 6 to 14 inches d.b.h., this zone extended out about 20 to 30 feet from the group.

TABLE I. *Estimated proportion (percentage) of ground surface covered by grass on plots in open areas near single trees and forest walls.* Longleaf pine forest type, southern Alabama. January 1950*

Average distance from trees (feet)	Near single tree	Near forest wall
13.2 (inside wall)	..	21
6.6 (inside wall)	..	20
6.6	48	33
13.2	55	41
19.8	55	47
26.4	55	47
33.0	55	50
39.6	53	51
46.2	53	50
52.8	54	50

*Average for 20 transects each for single trees (7 to 14 inches d.b.h.) and for forest walls (trees 6 to 14 inches d.b.h.). Each transect was made up of contiguous milacre plots.

Upland Tree Litter

As Wahlenberg, *et al.* (1939) have shown, tree litter smothers grasses and forbs. In the present study, herbage production on inventory plots was found to decrease rapidly as total tree litter increased. This decrease is expressed by the simple linear regression in Figure 2. Starting at an average of 1,000 pounds of herbage per acre where there was no tree litter, grass and forb production fell to about 260 pounds with 8,000 pounds of tree litter. The regression in Figure 2 accounts for 21 per cent of the variation in herbage production, so that total tree litter was more closely correlated with herbage production than was tree basal area (which accounted for only 14 per cent of the variation). Other observations have indicated that herbage production is higher under hardwood than under pine stands because pine litter builds up much greater weight than does hardwood litter (Campbell and Cassady 1951a).

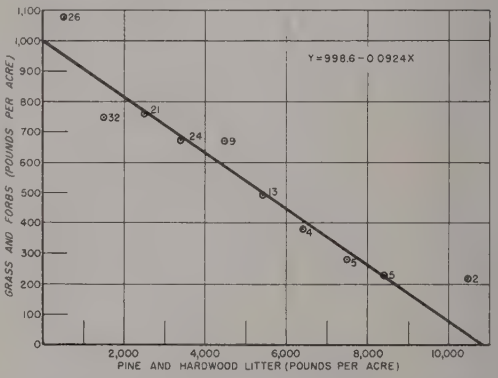

FIG. 2. Tree litter and herbage production (air-dry) on upland sites. Number of observations in average are beside each datum point.

Upland Soil Groups

Within the upland, there was a measurable difference in the herbage production on different soils.

Soil borings were made on each herbage plot. From these borings, soils were visually classed into five groups, which, for simplicity, were later reduced to three: soils with clay subsoils, sands or loams with loam subsoils, and deep sands. An analysis was made of the influence of these broad soil types on herbage production after the effect of litter weight was removed by covariance analysis.

The deep sands, mostly in the upland scrub oak type, produced an average of only 470 pounds of herbage per acre. The remaining uplands, in the longleaf pine type proper, had an average of 680 pounds of herbage per acre on areas with loam subsoils and 860 pounds per acre on areas with clay subsoils.

These differences in herbage production are highly significant, and litter and soil type together account for 31 per cent of the variation. Plots in each of the three soil groups had very similar correlation coefficient values and very similar regression coefficient values of forage production on litter weight.

High herbage production appeared to be a result of moisture conditions favorable to the growth of slender bluestem. On plots with 0 to 990 pounds of herbage per acre only 4 per cent of the forage was slender bluestem. Plots with 1,000 to 1,440 pounds per acre had 12 per cent of this species, and plots with 1,450 or more pounds per acre had 45 per cent. The highest herbage production on deep sand and on sand with loam subsoils was on lower slopes or swales, which had more moisture than the other upland sites. Clay subsoils are also valuable in maintaining relatively high soil moisture. All plots with 1,450 or more pounds herbage per acre had favorable moisture conditions, since they were in swales or at the toe of slopes or had clay near the surface.

Bottomland Sites

About 15 per cent of the Escambia Experimental Forest is in bottomlands. These bottomlands are more fertile than the uplands and produce a rank growth of bottomland hardwoods, brush, and slash pine that holds down the production of grass and forbs.

The 26 bottomland plots in this study—too few for statistical analysis—had an average production of 240 pounds of grasses and forbs and 300 pounds of brush foliage per acre (measurements included only brush foliage within 4.5 feet of the ground, considered as available for browsing by cattle). The 141 upland plots averaged 2.75 times as much herbage (720 pounds), and had only 120 pounds of brush foliage per acre.

Switchcanes made up nearly 25 per cent of the total grass weight, and Panicums another 20 per cent. Other forage species were the less palatable Muhlenbergias and sedges. Some of this bottomland forage is grazed in fall and winter, when upland species are unpalatable. However, the dense brush makes much of it inaccessible to cattle.

Herbage Production and Grazing Capacity

The foregoing data have a direct application in the better understanding of grazing capacity, and in attaining more effective use of forest land for combined timber growing and range cattle grazing in southern Alabama and adjacent areas. Herbage production can be translated directly into an estimate of grazing capacity, based on cattle utilization of approximately 40 per cent of the total grass herbage, and allowing about 20 pounds of forage (air dry weight) per adult animal per day. (Campbell and Cassady 1951b).

Soils have previously had little or no attention in estimating grazing capacity. However, in southern Alabama, this study showed that deep sands produced an average of 470 pounds of herbage per acre, equivalent to about 3.2 acres to graze one cow for one month. Soils with loam subsoils had an average of 680 pounds of herbage per acre, or a grazing capacity of about 2.2 acres per cow per month. Soils with clay subsoils produced an average of 860 pounds of herbage per acre, equivalent to about 1.75 acres per cow-month.

In addition to soil type, the tree stand and litter must be considered. Thus, upland areas having practically no trees and litter produced an average of 1,000 pounds of air-dry grasses and forbs per acre per year, or about 1.5 acres per cow-month. Moderately stocked forest, with about 90 trees over 4 inches d.b.h., with a basal area of 100 square feet, and about 5,000 pounds of litter per acre, produced an average of only 500 pounds of herbage or less, and required at least 3 acres per cow-month. In working out the practical grazing management for a specific area, many other features beyond the scope of this report require attention, such as seasonal grazing values and many forest management practices which can help to maintain forage production at higher levels than on unmanaged forest range.

Summary

A study was made in second-growth longleaf pine lands in southern Alabama to determine relationships between production of grasses and forbs and several ecological factors.

Herbage production decreased as the basal area of the tree stand increased. The curvilinear regression showing this relationship is highly significant, statistically, but accounts for only 14 per cent of the variation in herbage production. Distribution of the tree stand also affects herbage production. A single longleaf pine tree 7 to 14 inches d.b.h. influences grass production only 6 to 8 feet from the trunk, while a group of trees

reduces herbage production up to 20 to 30 feet away from the forest wall.

Weight of tree litter was closely associated with herbage production. The linear regression is highly significant, statistically, and accounts for 21 per cent of the variation in herbage production.

Three major upland soil groups were recognized in this study. The mean herbage production per acre (adjusted to average litter weight) by soil groups was: soils with clay subsoils—860 pounds, soils with loam subsoils—680 pounds; and deep sands—470 pounds. Soil groups and litter weight together account for 31 per cent of the variation in herbage production. Herbage production was highest on moist sites favorable to slender bluestem.

Uplands produced about 2.75 times as much grass as did the bottomlands. Since bottomland soils are basically more productive than upland soils, the difference is attributed to heavy brush and tree competition in the bottoms.

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THE RECURRENCE OF SPRUCE BUDWORM INFESTATIONS IN THE PAST CENTURY IN THE LAC SEUL AREA OF NORTHWESTERN ONTARIO[1]

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Introduction

The abundance of balsam fir, *Abies balsamea* (L) Mill., a climax constitutent of the boreal forest in North America, varies in different parts of eastern Canada (Halliday 1937). In recent years, epidemics of the spruce budworm, *Choristoneura fumiferana* (Clem.), have occurred in many areas supporting widespread stands of mature balsam fir. One of these areas is in the vicinity of Lac Seul in Northwestern Ontario, where an outbreak has been in progress for approximately the last 12 years; in 1952, this outbreak covered close to 10,000 square miles.

Although the spruce budworm feeds on both white spruce, *Picea glauca* (Moench) Voss., and balsam fir, the latter is more vulnerable, and usually succumbs after five years of severe defoliation (Belyea 1952), whereas white spruce may withstand an additional one to two years of attack (Swaine, Craighead, and Bailey 1924). In the wake of a spruce budworm outbreak most of the balsam fir trees of commercial size are usually destroyed, whereas a relatively large number of white spruce trees survive (Turner 1952).

In the course of studies on the current outbreak in the Lac Seul area, indications of a disturbance about 85 years ago were gained from a consistent ring suppression pattern at that time in old white spruce, and from the age-class distribution of balsam fir in the present stands. This paper presents evidence that the disturbance is attributable to spruce budworm. The conditions of the forest preceding and following the past infestation, the area of origin and of spread, and the geographical relationship between the past and present infestations are described.

Evidence That the Past Disturbance Was Caused by Spruce Budworm

Methods

Swaine *et al.* (1924) showed that the characteristic retardation of the annual rings caused by spruce budworm defoliation can be used to trace

[1] Contribution No. 85, Division of Forest Biology, Science Service, Department of Agriculture, Ottawa, Canada.

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earlier outbreaks. Almost without exception, white spruce trees one hundred years of age or older growing in the general region of Sioux Lookout in northwestern Ontario show a characteristic ring suppression pattern about 85 years ago (Fig. 1).

FIG. 1. Section of a disc from a white spruce tree showing the suppressed ring pattern at the time of the disturbance of 1867-1877.

Increment cores were obtained from old white spruce trees in 81 localities over an area of approximately 20,000 square miles in northwestern Ontario. In most localities, cores were obtained from at least 10 trees, but, owing to the scarcity of old white spruce trees, fewer cores were obtained in some localities. Supplementary discs were taken from some of the more accessible points. Each core was examined for a suppression pattern between 1850 and 1885. Ring widths during this period were measured with the aid of a binocular microscope equipped with an ocular micrometer, the average ring width for each year for all trees from each locality was computed and the results were plotted. Only living trees were sampled so that the outside ring could be dated. The 1857 growth was nearly always a narrow ring throughout the area studied and this "marker ring" provided an additional check.

Five plots were studied intensively near the geographical centre of the past disturbance for the purpose of reconstructing stand histories. Plot 1 was one-fifth acre while the others were one-tenth. The plots were more or less evenly distributed along a 20-mile stretch of the Red Lake Road. All the plots were located in overmature coniferous stands varying between 150 and 175 years of age. In all cases the stands were established after fire.

Records are available of the soil type and the ground vegetation for each plot. Windthrown trees were recorded as to species, diameter, and degree of decay. All the standing trees were cut and records taken of the species, diameter at breast height (four and one-half feet from the ground), diameter at stump height 85 years ago, present total height, total height 85 years ago, age at ground level, and time and number of years of suppression if suppression occurred. The diameter, 85 years ago, was calculated by measuring the distance from the centre of the tree to the 1867 year of growth, and the total height 85 years ago was obtained by cutting through the stem at various levels and counting the annual rings until that point was reached where the number of rings was exactly 85.

RESULTS

Table I gives the individual and average width of the rings over the years 1852 to 1882 for the increment cores for each of ten trees from Wapesi Lake, a locality about 30 miles northwest of Sioux Lookout. This shows that there is a certain amount of variability in the width of rings between cores but that the trends are fairly uniform, especially during the years of suppression. For instance, 1867 appears as the first year of suppression in all trees and 1871 as the year of the severest suppression in each tree. This constancy of pattern within the same locality did not hold in all localities studied. By obtaining the average yearly ring width for each locality, these differences tended to be minimized.

Figure 2 shows the average yearly radial growth from 1850 to 1880 based on 13 white spruce, 15 white pine, *Pinus Strobus* L., and 15 red pine, *Pinus resinosa* Ait., at Cedar Lake, 55 miles west of Sioux Lookout. It can be seen that the growth patterns of the three species are in fairly good accord, except for the marked suppression in white spruce that began about 1867 and reached its greatest severity in 1871. Unlike the decline that began in the latter part of the 1850 decade, this period of suppression in the spruce was not reflected in the growth of the other species, and therefore was not the result of an overriding factor, such as weather.

The first year of suppressed growth in the sequence of continuous growth decline is considered as the first year of suppression. The year of initial suppression varies from one area to the next, indicating that the disturbance had spread from a centre. Figure 3 shows the average yearly radial growth from 1850 to 1880 for 10 white spruce trees in each of six different localities.

TABLE I. *Width of rings and average width of rings in mm. from 1852 to 1882 of increment cores from ten different white spruce trees from Wapesi Lake.*

Year	Core Number										Average
	1	2	3	4	5	6	7	8	9	10	
1852....	2.0	1.8	1.5	3.2	3.7	1.8	2.1	2.9	2.8	5.0	2.7
1853....	1.9	1.7	1.5	3.0	3.5	1.5	2.2	3.0	2.5	4.8	2.6
1854....	1.7	1.4	1.6	3.1	3.0	1.6	2.0	3.0	2.0	3.9	2.3
1855....	1.8	1.8	1.9	2.8	2.2	2.0	1.8	2.0	2.1	4.0	2.2
1856....	1.6	1.5	1.8	2.8	3.2	2.0	1.5	2.7	2.4	4.2	2.4
1857....	1.2	1.1	1.4	2.1	2.3	1.5	1.0	2.0	1.8	3.0	1.7
1858....	1.5	1.5	1.5	2.3	3.0	1.7	1.7	2.9	2.2	3.0	2.1
1859....	1.3	1.5	1.9	2.2	2.5	1.5	2.0	2.5	2.3	2.8	2.1
1860....	1.2	1.9	1.9	2.3	3.3	1.6	2.0	3.2	2.1	3.1	2.3
1861....	2.1	2.4	2.3	2.7	3.0	2.0	2.5	3.2	2.8	3.2	2.6
1862....	2.0	2.0	2.1	2.8	3.0	2.1	2.5	2.8	2.7	3.6	2.6
1863....	2.0	1.9	1.7	3.1	2.7	1.7	2.5	2.2	2.4	2.7	2.3
1864....	1.6	1.6	1.5	2.5	2.5	1.6	2.5	2.5	2.1	2.7	2.1
1865....	1.6	1.7	1.7	2.7	2.7	1.9	2.3	2.5	2.3	3.3	2.3
1866....	1.7	2.0	1.8	2.7	2.4	2.0	2.3	2.5	2.6	2.7	2.3
1867....	1.2	1.4	1.4	1.5	2.0	1.5	2.0	2.3	1.6	2.0	1.7
1868....	0.9	1.3	1.5	1.7	2.2	1.3	1.6	2.4	1.5	2.0	1.6
1869....	0.9	1.2	1.4	1.5	1.5	1.1	1.5	1.5	1.3	2.0	1.4
1870....	0.7	0.8	0.8	1.2	1.2	0.7	1.3	1.7	1.1	1.3	1.1
1871....	0.3	0.4	0.5	1.0	1.0	0.7	1.1	1.4	0.9	1.3	0.9
1872....	0.3	0.5	0.7	1.4	1.8	0.8	1.2	1.8	1.0	1.6	1.1
1873....	0.4	0.6	1.4	1.5	1.8	1.2	1.4	1.8	1.3	1.9	1.3
1874....	0.3	0.7	1.3	1.7	1.9	1.0	1.6	1.9	1.3	1.9	1.4
1875....	0.6	1.0	1.7	1.7	2.2	1.4	1.8	1.9	1.6	1.7	1.6
1876....	0.9	0.9	1.5	1.5	2.0	2.0	1.8	2.2	1.7	2.0	1.7
1877....	1.0	1.0	1.8	1.5	2.2	1.5	1.8	2.7	1.6	1.8	1.7
1878....	1.0	1.2	2.0	1.7	2.5	1.8	2.3	3.0	2.1	1.9	2.0
1879....	1.3	1.2	1.7	1.5	1.6	1.6	1.7	2.2	1.9	1.4	1.6
1880....	1.0	0.7	1.5	1.4	1.5	1.1	1.4	2.0	1.7	1.7	1.4
1881....	1.3	1.1	1.5	1.4	1.7	1.2	1.8	2.5	1.8	1.8	1.6
1882....	1.1	1.1	1.5	1.7	2.2	1.4	2.1	2.5	1.9	2.2	1.7

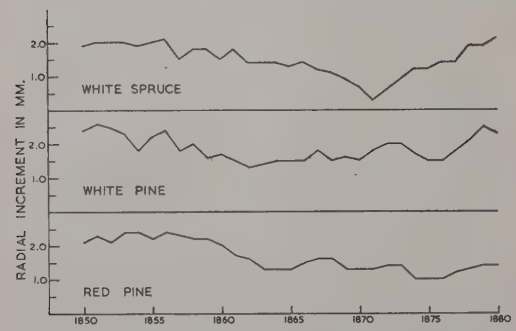

FIG. 2. Average yearly radial growth from 1850 to 1880 for 13 white spruce *Picea glauca* (Moench) Voss., 15 white pine, *Pinus Strobus* L., and 15 red pine, *Pinus resinosa* Ait., at Cedar Lake. The white spruce show a distinct suppression for the period 1867-1874.

Minnitaki Lake and Tully Lake are near the centre of the past disturbance, Basket Lake and Canyon Lake are at intermediate points east and west of the centre, Cobble Lake and Sowden Lake are at the eastern and western boundaries of the disturbance.

Table II gives the basal area of living trees, by species, for the lines cruised at each of the six plots studied. In the case of plots 3, 4 and 5, a

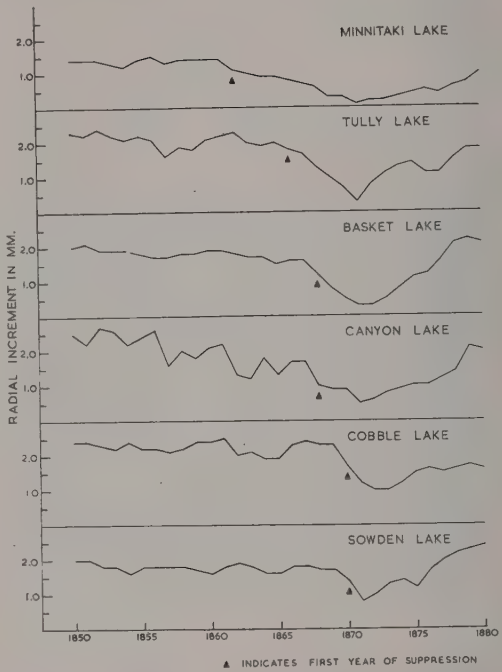

FIG. 3. Average yearly radial growth from 1850 to 1880 for 10 white spruce trees from each of six different localities indicating that the first year of suppression varied from one locality to the next. Minnitaki Lake and Tully Lake are near the centre of the past disturbance, Basket Lake and Canyon Lake are at intermediate points east and west of the centre, Cobble Lake and Sowden Lake are at the eastern and western boundaries of the disturbance.

TABLE II. *Basal area in square feet per acre of living trees,* and per cent of total basal area for lines cruised at each plot.*

Plot Number		Tree Species†							
		Bf	SW	Sb	Pj	Po	Bw	Cw	Total
1	B. A./Acre.....	50	17	13	10	19	5	0	114
	% of B. A.....	43.8	14.9	11.4	8.8	16.7	4.4	0	100
2	B. A./Acre.....	50	11	0	0	3	22	0	86
	% of B. A.....	58.1	12.8	0	0	3.5	25.6	0	100
3	B. A./Acre.....	19	13	1	10	12	8	13	76
	% of B. A.....	25.0	17.1	1.3	13.2	15.8	10.5	17.1	100
4	B. A./Acre.....	66	17	17	0	13	5	0	118
	% of B. A.....	55.9	14.4	14.4	0	11.0	4.3	0	100
5	B. A./Acre.....	25	12	45	6	1	6	0	95
	% of B. A.....	26.4	12.6	47.4	6.3	1.0	6.3	0	100

*In the case of balsam fir and white spruce, the basal area of trees recently killed by the spruce budworm was included.

† Bf - Balsam fir, *Abies balsamea* (L.) Mill.
Sw - White spruce, *Picea glauca* (Moench) Voss.
Sb - Black spruce, *Picea mariana* (Mill.) BSP
Pj - Jack pine, *Pinus Banksiana* Lamb.
Po - Trembling aspen, *Populus tremuloides* Michx.
Bw - Paper birch, *Betula papyrifera* Marsh.
Cw - White cedar, *Thuya occidentalis* L.
La - Larch, *Lariz laricina* (Du Roi) K. Koch.

number of balsam fir and white spruce trees had recently been killed as a result of current spruce budworm defoliation. For the purpose of determining the stand composition prior to recent budworm damage, these trees were included in the calculations of basal area. Table II shows that the stands were essentially coniferous with balsam fir and white spruce being the predominant species, except for plot 5 where black spruce, *Picea mariana* (Mill.) BSP, was predominant.

In Table III, the number of stems of all species is given by diameter classes for living and dead trees and the total number of stems per acre on the lines cruised. Most of the dead balsam fir and white spruce trees in plots 3, 4 and 5 were recently killed by budworm. In the case of other species, mortality resulted from suppression or overmaturity. Table III shows that in plots 1, 2, 3, and 4, balsam fir was predominant, especially in the lower diameter classes that form the understories. In plot 5, balsam fir was next in abundance to black spruce. A much greater percentage of the jack pine and poplar trees were dead than is shown by the ratio of dead stumps to living trees, since many of the dead trees were windthrown. In this area, fires are usually followed by the sub-climax species—poplar on the deep clay soils and jack pine on the shallower or sandy soils. These give way to the climax stands of balsam fir and white spruce. In all the plots the transition to a climax forest was almost complete, with relatively few remnants of the sub-climax still surviving.

Table IV gives the time at which balsam fir

TABLE III. *Number of stems of all species by diameter classes and total number of stems per acre on lines cruised for each plot.*

Plot Number	D. B. H. in inches*	Bf		Sw		Sb		Pj		Po		Bw		Cw		La†	
		L.‡	D.	L.	D.	L.	D.	L.	D.	L.	D.	L.	D.	L.	D.	L.	D.
1	1-5	777	68	26	1	80	5	..	..	3	..	4	1	..	..	..	..
	6-10	213	19	11	4	63	5	19	41	2	3	21	9	..	..	..	..
	11-15	13	1	15	4	4	..	12	15	13	9	2	..	..	..	..	..
	16-22	..	..	9	..	..	..	2	..	13	9	..	..	..	..	..	..
	Total stems tallied	1003	88	61	9	147	10	33	56	31	21	27	10	..	..	..	..
	Total stems per acre	501	44	30	4	73	5	16	28	15	10	13	5	..	..	..	..
2	1-5	675	57	36	1	..	..	..	..	2	1	12	2	..	..	..	..
	6-10	202	16	13	7	..	2	..	..	3	4	65	32	..	..	..	..
	11-15	12	..	11	1	2	..	..	..	5	11	29	3	..	..	..	..
	16-22	..	..	5	..	..	..	..	..	..	1	..	2	..	..	..	..
	Total stems tallied	889	73	65	9	2	2	..	..	10	17	106	39	..	..	..	..
	Total stems per acre	444	36	32	4	1	1	..	..	5	8	53	19	..	..	..	..
3	1-5	575	267	4	3	1	..	..	..	3	1	28	22	36	..	..	..
	6-10	15	36	11	21	8	..	9	18	9	18	35	26	59	..	..	..
	11-15	..	..	7	8	1	..	18	21	12	4	3	2	3	..	..	..
	16-22	..	..	1	..	..	..	4	..	5	3	..	..	..	..	..	..
	Total stems tallied	590	303	23	32	10	..	31	39	29	26	66	50	98	..	..	..
	Total stems per acre	295	151	11	16	5	..	15	19	14	13	33	25	49	..	..	..
4	1-5	21	419	..	..	26	8	..	..	..	..	..	..	..	..	..	..
	6-10	4	292	..	12	107	16	..	2	1	1	8	6	..	..	..	..
	11-15	..	20	2	9	2	..	..	3	12	6	8	..	..	..	..	..
	16-22	..	..	1	8	..	..	..	..	8	4	..	..	..	..	..	..
	Total stems tallied	25	731	3	29	135	24	..	5	21	11	16	6	..	..	..	..
	Total stems per acre	12	365	1	14	67	12	..	2	10	5	8	3	..	..	..	..
5	1-5	197	32	3	2	282	12	..	..	..	..	2	1	..	..	10	90
	6-10	54	35	2	11	161	13	2	17	1	1	10	8	..	..	1	50
	11-15	10	8	4	3	16	2	7	24	1	2	8	4	..	..	..	..
	16-22	2	1	4	3	..	..	4	7	1	1	..	..	..	..	..	..
	Total stems tallied	263	76	13	19	459	27	13	48	3	4	20	13	..	..	11	140
	Total stems per acre	131	38	6	9	229	13	6	24	1	2	10	6	..	..	5	70

*Diameter at breast height, *i.e.* at 4½ feet from the ground. †See footnote Table II. ‡L - Living. D - Dead.

trees over one-half inch in diameter at breast height became established in the plots studied. In plots 1 and 3 all balsam fir trees over one-half inch in diameter were over 85 years old. This indicates that no balsam fir trees became established in these plots for many decades after 1867. In the other three plots, 50 per cent or more of the balsam fir trees were found to antedate the time of the disturbance. The remainder of the balsam fir trees became established in the ten years that followed the disturbance; after that, no fir trees became established until recent times.

A large number of balsam fir trees less than one-half inch in diameter (seedlings) occur on each of the five plots. Regeneration studies that are being carried out in the immediate vicinity of these five plots show a range of from 3,000 to 7,000 balsam fir seedlings per acre. Over 96 per cent of the specimens encountered were less than 20 years and very few were more than 35 years old.

Table V shows the 1861-67 distribution by height class of the balsam fir trees that were studied in each plot. Of a total of 144 trees that survived the past infestation, 68 per cent were two feet in height or less, only 3 per cent were over 11 feet high, and none were over 24 feet high 85 years ago.

TABLE IV. *Time at which balsam fir trees over one-half inch D.B.H.* became established for each plot studied.*

Plot Number	1800-1850	1851-1860	1861-1867	1868-1880	1881-1890	1891-1900	1901-1950
1	21 45%	14 30%	12 25%	0	0	0	0
2	0	1 3%	16 44%	19 53%			
3	18 56%	5 16%	9 28%	0	0	0	0
4	0	1 3%	20 55%	14 42%			
5	1 2%	11 27%	16 40%	13 31%	0	0	0

*Diameter at breast height, *i.e.*, at 4½ feet from the ground.

TABLE V. *Distribution by height class of currently standing balsam fir trees at the time of the past disturbance.*

Plot Number	Height in feet					
	0-2′	3′-5′	6′-8′	9′-11′	12′-14′	21′-24′
1	24	12	5	4	2	0
2	17	0	0	0	0	0
3	9	8	9	2	0	3
4	21	0	0	0	0	0
5	26	2	0	0	0	0
Total	97	22	14	6	2	3
Per Cent	68	15	10	4	1	2

Discussion

Since the radial growth patterns for the different species of trees in the Sioux Lookout area are similar except for a period starting about the year 1865 when white spruce trees show a marked suppression, this indicates that for a number of years some factor was affecting the growth of this species adversely, while not affecting the growth of the pines. Furthermore, the age-class distribution of balsam fir trees shows that no additional trees of this species became established for some forty years following the time of the radial growth suppression in white spruce, indicating that all or nearly all the seed-bearing balsam fir trees were destroyed at that time. Only a severe and prolonged spruce budworm outbreak can logically be held responsible. In plots 1 and 3, no balsam fir trees over one-half inch in diameter were found to be younger than 85 years but in the other three plots mortality of at least some of the seed bearing trees was delayed for approximately 10 years, as shown by the fact that some balsam fir became established in that interval of time (Table IV). Swaine *et al.* (1924) found that weakened trees may die as late as five to ten years after a budworm epidemic.

The height-class distribution of balsam fir trees, at the time of the past infestation, indicates that those trees that survived the past infestation were mostly in the seedling stage (Table V).

Conditions similar to those found in the wake of several recent outbreaks seem to have prevailed 85 years ago, namely, that all, or nearly all, the balsam fir trees of merchantable size were killed, but that many of the seedlings and some of the saplings survived. Present conditions in plot 4 may be taken as typical of conditions existing in the areas where heavy mortality of balsam fir has resulted from recent budworm defoliation. In this plot, about 97 per cent of the balsam fir trees of merchantable size have been killed by the budworm in the last few years (Table III), yet over 3,000 living balsam fir seedlings per acre were found.

Extent, Area of Spread, and the Geographical Relationship of the Past Infestation to the Present Infestation

Figure 4 shows the localities where the suppressed ring pattern in white spruce trees was observed and where it was absent. The east, north and west boundaries of the past infestation

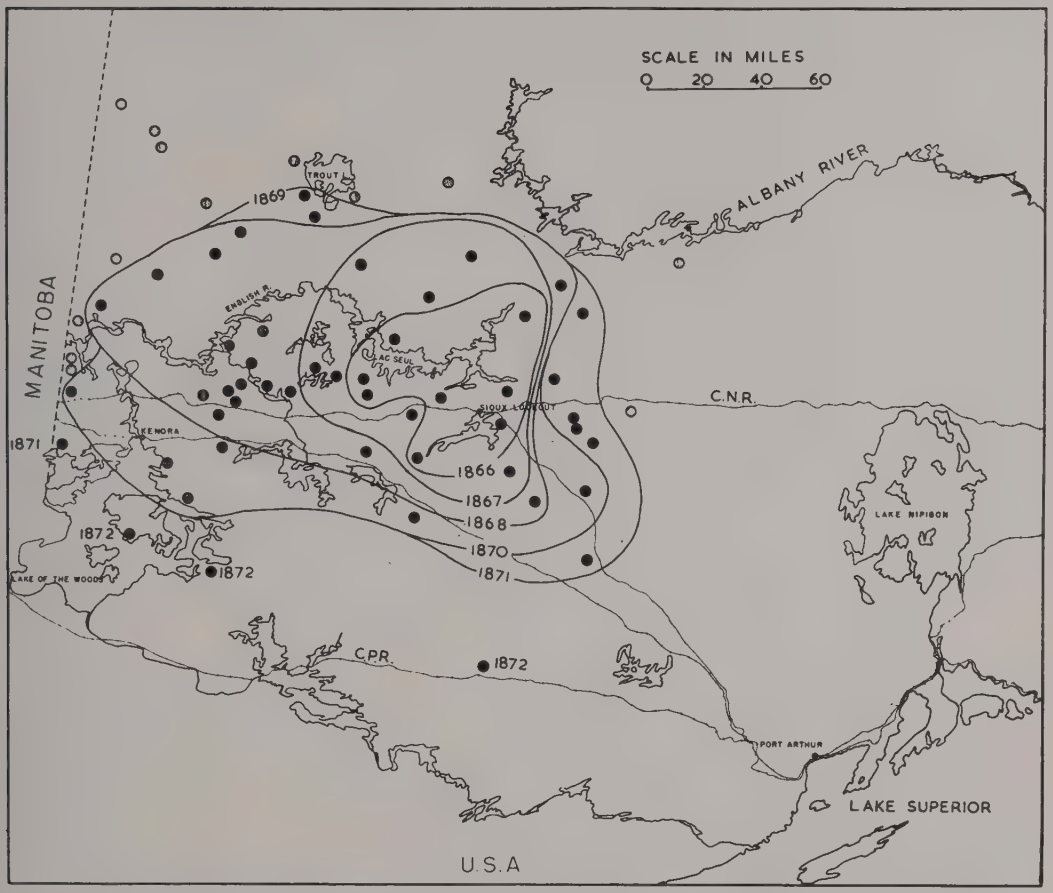

FIG. 4. Area in northwestern Ontario where a severe spruce budworm outbreak occurred about 1866. The solid dots indicate localities where a ring suppression pattern in white spruce trees was observed and the other dots indicate the localities where no pattern was observed. These localities having the same first year of suppression are enclosed within isolines.

are determined by a number of points where no suppression pattern occurred. Several days of aerial exploration failed to reveal any mature stands of white spruce to the south, where stands of jack pine, poplar or younger spruce and fir following relatively recent fires are predominant. The southern boundary of the infestation is therefore not accurately defined. Ring suppression patterns in old white spruce trees were obtained from two points on the east shore of the Lake of the Woods and from one point considerably farther south. These indicate that budworm defoliation occurred, at least in some isolated pockets, almost as far south as the international boundary.

The area encompassed by the old infestation covered approximately 10,000 square miles. However, the outbreak was probably not equally heavy throughout this entire area since spruce budworm outbreaks are confined to stands of spruce and balsam fir. Owing to topographic and edaphic conditions, such stands do not form a continuous forest over this area.

In Figure 4, all localities having the same first year of suppression are enclosed within isolines. These cannot be considered as absolute lines of demarcation for the successive years of defoliation; they are but approximations. Several points in the neighbourhood of Sioux Lookout and the eastern portion of Lac Seul show 1866 as the first year of suppression, indicating that the infestation had its origin in this vicinity. Within this area, the first apparent year of suppression was as early as 1862 in two localities. However, in both these localities the white spruce trees sampled were very old and showed poor diameter growth for approximately the last 100 years, thus

obscuring to some extent the initiation of suppression caused by the spruce budworm (see data for Minnitaki Lake, Fig. 3). From this area of origin the infestation spread mostly westward until by 1870 and 1871 it reached points close to the Manitoba boundary.

The relationship between defoliation and reduction in diameter growth in white spruce was studied in two localities where budworm defoliation has been carefully recorded since the beginning of the present infestation. Increment cores were taken from 25 white spruce trees from each locality and the last 20 years of radial growth were measured in the manner described earlier. The computed averages show the first year of ring suppression, for one locality, as having occurred three years after the beginning of the infestation, and, for the second locality, one year later. Though more work is required to determine the exact relationship between spruce budworm defoliation and reduction in increment in white spruce, it can be reasonably assumed that the first year of ring suppression may occur three or four years after the budworm has reached epidemic proportions. Thus the past infestation quite possibly started three or four years earlier than is indicated by the first year of ring suppression in the white spruce trees studied in the different localities.

The fact that there is an interval of a few years between the beginning of an outbreak and the beginning of suppression permits the use of subsidiary data to support foregoing arguments for a major infestation. Since general suppression in spruce began about 1866-67, the outbreak presumably began about 1862-64, or even earlier. Previous work (Wellington *et al.* 1950; Wellington 1952) has demonstrated that there is a pre-outbreak period in which summer droughts recur. This period usually amounts to three or four years,

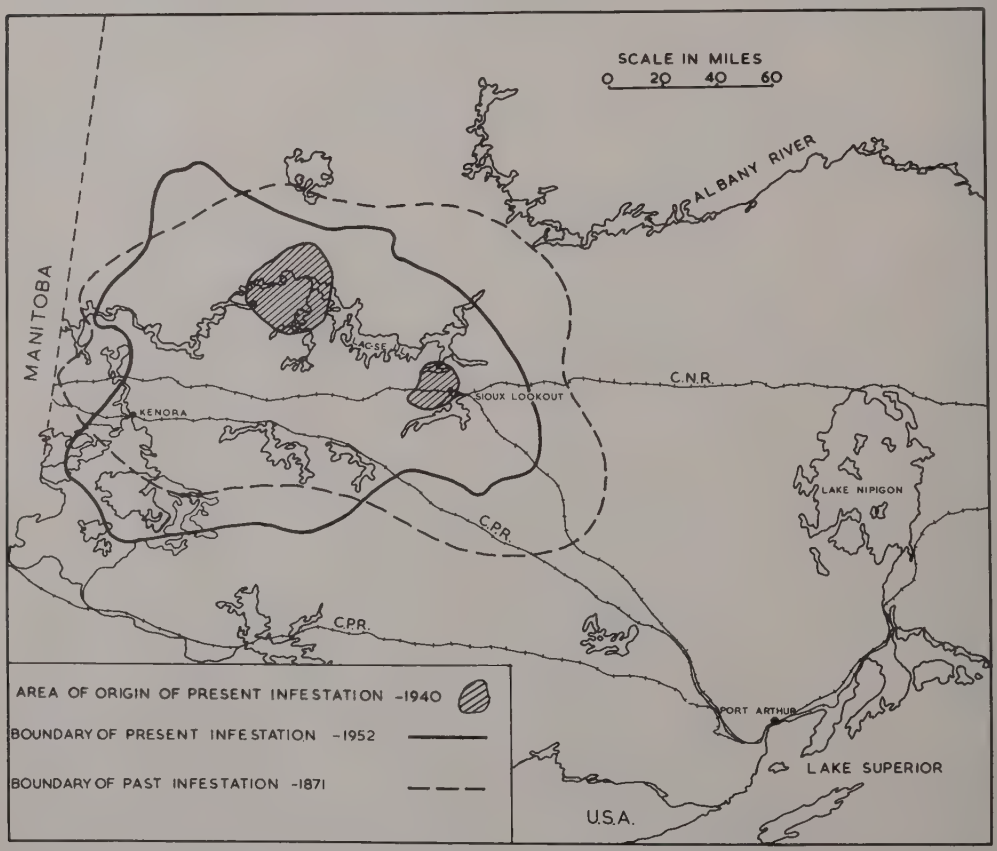

FIG. 5. Area in northwestern Ontario where a past spruce budworm infestation has occurred and where a current infestation is taking place.

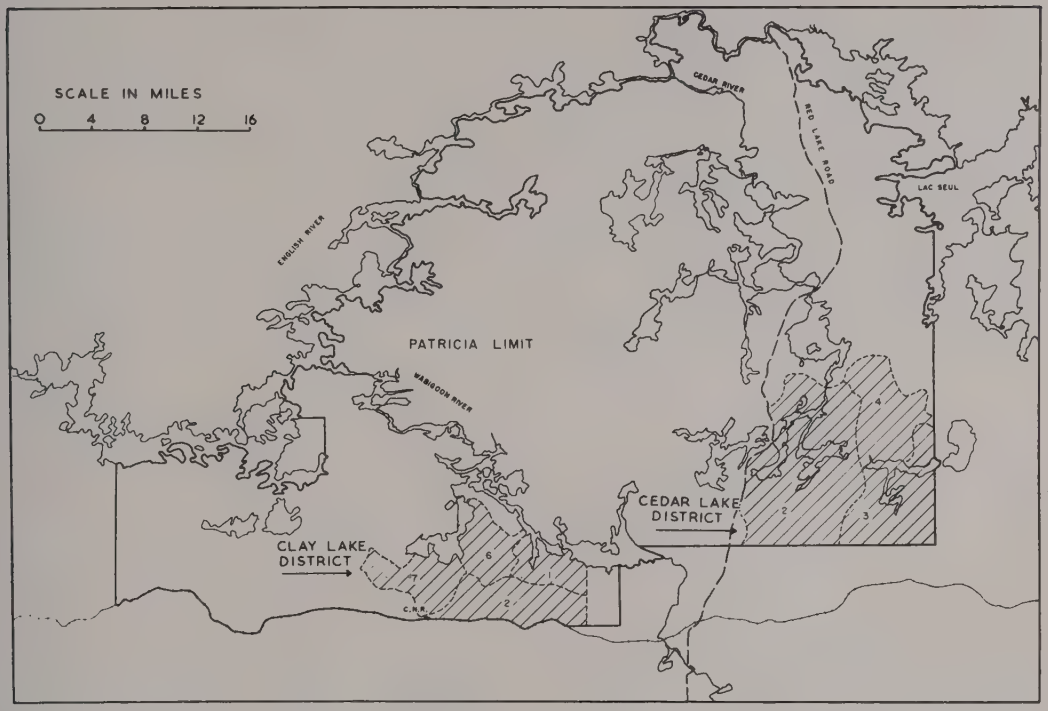

FIG. 6. The Patricia Concession in northwestern Ontario, showing the Clay Lake District and the Cedar Lake District watersheds (cross hatched) where timber surveys were carried out in 1926 and 1948.

and further adjustment of the tentative dates above by this amount gives 1858-60 as the possible beginning of such a pre-outbreak period. Figure 2 shows clearly that there was a decline in the growth of both spruce and pines from the latter half of the 1850's through the early 1860's, and such prolonged general declines result chiefly from climatic change. Consequently, there is good evidence for a climatic trend during this period similar to that which preceded several more recent spruce budworm outbreaks.

Figure 5 shows the areas of origin, the present boundary of the current infestation, and the boundary of the past infestation. The present infestation had two centres of origin, one near Sioux Lookout, in the same vicinity as the apparent centre of origin of the old infestation, and the other about 60 miles farther west near Wabashkang Lake and the English River.

The boundaries of the current infestation have been mapped every year since 1945. Until 1951, the infestation had spread mostly westward and southward from the western centre of origin and had by then covered approximately 5,000 square miles. In 1952, the area was greatly increased, mostly to the east and to the south, and now covers close to 10,000 square miles. The area currently infested is remarkably similar to that of the old infestation.

Changes in the Balsam Fir Content of the Forest in the Last 25 Years in Relation to the Past and Present Spruce Budworm Outbreaks

A timber survey of a section of the infested area known as the Patricia Concession (Fig. 6) was carried out about 25 years ago and, more recently, parts of the Cedar Lake and Clay Lake Districts of this concession were resurveyed. Data from these surveys provided an excellent opportunity of assessing changes of forest composition in the last 25 years.

Table VI gives the amount in cords of merchantable spruce and balsam fir for the different watersheds in the Cedar Lake and Clay Lake Districts, as assessed during the surveys of 1926 and 1948. In the Clay Lake District, which comprises over 45,000 acres in land area, the volume of spruce increased by 1 per cent and the volume of balsam fir by 265 per cent over a period of 22 years. In the Cedar Lake District, which comprises over 80,000 acres in land area, spruce decreased in volume by 16 per cent and balsam fir increased by 366 per cent during the same period.

The reduction in spruce in the Cedar Lake District might be explained by the fact that one-half of the land area is occupied by overmature or decadent stands where natural mortality is high and windthrow of large trees is prevalent. Grouping the two districts, spruce shows a reduction of 12 per cent and balsam fir an increase of 337 per cent over an area of approximately 125,000 acres. It is evident that the increase in the merchantable volume of balsam fir in the last 25 years has been very considerable.

TABLE VI. *Amount in cords of merchantable* spruce and balsam fir for the periods of 1926 and 1948 in the Clay Lake and Cedar Lake District watersheds.*

District	Watershed	Land Area in Acres	White and Black Spruce		Balsam fir		
			1926	1947	1926	1947	
Clay Lake	1.....	12,900	35,600	46,900	2,900	13,000	
	2.....	16,877	56,200	62,900	4,800	14,900	Spruce increased by 1%
	6.....	7,239	33,000	28,000	1,900	3,100	
	7.....	8,749	51,600	40,500	1,700	10,200	Balsam fir increased by 265%
	Total..	45,765	176,400	178,300	11,300	41,200	
Cedar Lake	2.....	39,562	333,500	251,300	16,500	66,000	Spruce decreased by 16%
	3.....	21,451	90,600	97,800	7,800	31,500	
	4.....	19,366	107,600	95,700	3,500	32,100	Balsam fir increased by 366%
	Total..	80,379	531,700	444,800	27,800	129,600	
Grand Total..		126,144	708,100	623,100	39,100	170,800	Spruce decreased by 12% Balsam fir increased by 337%

*Trees 5 inches and over in diameter at breast height.

Previous studies (Blais 1952) have shown that mature or flowering balsam fir trees are important in providing conditions favourable to the increase of populations of the spruce budworm and that, thereby, they contribute to the initiation and spread of spruce budworm epidemics. The large percentage of balsam fir trees that became established prior to the infestation of 1865 provides evidence that there were extensive stands of seed-bearing fir trees at that time. These mature trees succumbed to the old infestation, and it was not until recent years, when the surviving seedlings reached maturity, that spruce budworm populations were again able to reach epidemic proportions. The passing of approximately 70 years (the interval between the past and present infestations) was required for the development of a new forest capable of supporting another destructive outbreak of the spruce budworm. Since the exploitation of the timber resources of this portion of Ontario has begun only very recently, any changes in forest composition that have taken place, and any phenomena connected with these changes can be considered as being completely natural.

In addition to stating that spruce budworm epidemics can develop only when there is sufficient balsam fir, Swaine *et al.* (1924) suggests that the older epidemics followed the course of logging operations, becoming more extensive as exploitation proceeded farther into virgin forests. The present studies do not support this view since they indicate that severe and widespread spruce budworm infestations occurred in virgin forests. They are more in agreement with the suggestion of Graham and Orr (1940) that outbreaks of the spruce budworm have occurred in the past at intervals of from 40 to 70 years and that such intervals represent the period required for a generation of balsam fir to reach a dominant position in the forest stands.

SUMMARY AND CONCLUSIONS

Evidence that a widespread and destructive spruce budworm outbreak occurred in the latter half of the nineteenth century in northwestern Ontario was gained from the characteristic reduction of the annual ring increment in old white spruce and by the age-class distribution of balsam fir. The past outbreak had its centre of origin in the Sioux Lookout area and spread over a territory encompassing 10,000 square miles in a period of about 7 years.

The same conditions that were found in the wake of several recent outbreaks seem to have prevailed 85 years ago, namely, that all or nearly all the balsam fir trees of merchantable size were killed, but many of the seedlings and some of the saplings survived.

The large number of balsam fir trees that became established prior to the infestation of 1865 give evidence that there were extensive stands of seed-bearing fir trees at that time. These parent trees were destroyed during the past infestation and it was not until recent years, when their progeny reached maturity, that spruce budworm populations again reached epidemic proportions.

Since the forests in this area had never been subjected to exploitation, all changes in the forest composition and all related phenomena are entirely natural. Spruce budworm outbreaks, therefore appear to be a phase in a natural cycle of events associated with the maturing of balsam fir.

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SOME RELATIONSHIPS OF EVAPORATION RATE TO VAPOR PRESSURE DEFICIT AND LOW WIND VELOCITY

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Introduction

Standardized evaporimeters are commonly used in approximating relative evaporation potentials in plant environments (Fuller 1911, Weaver 1914, Bode 1920, Gates 1921, Cain and Friesner 1929, Costello 1931, Livingston, B. E., 1935, Aikman and Smelser 1938, Livingston, R. B., 1949). Since this potential is a measure of atmospheric conditions as a whole, rather than of factors interpreted separately, water loss data are an expression of sum effects.

The vapor pressure deficit, as a measure of atmospheric humidity, is an indirect measure of evaporation. This function, also called the saturation deficit, is equal to the difference between the saturation vapor pressure at a given air temperature and the actual vapor pressure at the same temperature. As the air approaches saturation, the atmospheric deficit decreases, as does the possible water loss from the immediate plant and soil environment. With increasing aridity of the air, calculated values of the vapor pressure deficit assume greater magnitude indicating greater evaporation stresses. Since surface temperatures and corresponding vapor pressures are an important consideration in equating the evaporation rate, the accuracy of the vapor pressure deficit as a correlative function depends on the degree of temperature correspondence between the air and evaporating surface. Seldom are these values the same under most conditions. Penman (1948) determined evaporation from bare soil, grass, and open water relative to vapor pressure differences, in which he proposed a method of eliminating the difficult measurement of surface temperature. The limitations of the vapor pressure deficit have been discussed by Leighly (1937) and Thornthwaite (1940). Under certain conditions evaporation may be independent of the calculated deficit. For small surfaces, however, whose temperatures would follow closely those of the air, Gordon (1940) proposed that a high correlation is possible between evaporation and the vapor pressure deficit of the atmosphere.

Considering these points of view, it is the purpose of this study to determine the statistical relationship of evaporation rate to the vapor pressure deficit.[1] Included also in this study is the component effect of air movement as an evaporation factor.

Procedures

The study was conducted during July and August, 1951, for a period of five weeks. Two stations were selected, one in an open bluegrass pasture in full sunlight at all times during the day, the other beneath the canopy of a nearby hickory (*Carya*) grove. The latter station was placed so as to be in constant shade as much as possible, thus tending to eliminate rapid temperature changes due to sun flecks. Stand density averaged 41 trees per 100 M^2, or approximately 200 per

[1] The author expresses his appreciation to the University of Missouri Research Council in making available funds for this study, URC Project No. 304, 1951, and to Professor B. H. Frame who reviewed some of the data.

acre. There was no woody understory, and only a limited ground vegetation was present. The selection of these contrasting plant environments made possible a greater range of physical data, and also served as a basis for measuring canopy effects on evaporation and related factors. The sites were approximately 75 meters apart on a flat to gently sloping south aspect.

Each station was equipped with a louvred, white-painted shelter in which were placed a hygrothermograph, and maximum and minimum thermometers. Triplicate black and white Livingstone type atmometers with burette attachments were arranged around the shelter at a distance of approximately 1.5 meters. A Weather Bureau cup anemometer installed on the west side of each shelter completed the equipment. All instruments including those in the shelters were about 35 centimeters above ground level.

In order to evaluate the diurnal variation, water-loss readings were taken for periods ending at 6 a.m., 12 noon, and 6 p.m., beginning July 9 and continuing to August 17. At these times air movement was recorded for the interval just ended. Hygrothermographs were checked frequently with an aspirating psychrometer, operated within the shelter. Maximum and minimum thermometer readings served as an added check against corresponding chart temperatures. Evaporation values were discarded for periods during which precipitation occurred. Short-period measurements, usually of one hour duration, were made frequently for obtaining additional data using the aspirating psychrometer and a Biram anemometer. Water losses were read from the burettes to 0.2 cc.

A single station was set up for two weeks in August, 1952. Altogether 660 white-bulb readings were taken during rainless periods, 586 in 1951, the remainder in the following year. A similar number of black-bulb readings were made, although these are not discussed in the present paper.

Each of triplicate atmometer readings for the period was corrected to standard, summed, and a mean determined as cc. per hour. Temperature and humidity values were taken from recording charts for each two hour interval, and from which a vapor pressure difference was calculated using psychrometric tables. Individual pressure differences or deficits based on each two hour interval were summed and averaged to obtain a mean for the period. It is noted that a deficit was determined for each temperature and corresponding humidity rather than on the basis of the average temperature and humidity for the diurnal period. Separate calculations were made because of the non-linear relationship of temperature to vapor pressure in saturated air, which if performed otherwise would cause variation in the final results. Wind mileage for each period was converted to miles per hour (1 mph = 0.45 meters/sec.). Wind data were resolved later into the following classes: 0.00-0.49; 0.5-2.49; 2.5-4.49; and 4.5-6.49(7.1). A single value, 7.1, the largest mean velocity determined during the study, is included in the last wind class. Wind values represent merely the mean velocity for the period. They do not indicate necessarily that wind speeds did not prevail which were either higher or lower than the class limits between which the mean fell.

Factor Relationships

Figure 1 shows the association of evaporation rate to the vapor pressure deficit and to wind, *in toto,* and by velocity classes. Within the range of data obtained, this relationship would appear to be linear, and is expressed by the following multiple regression:

Evap. = −0.18 cc. + 0.125 v.p.d. + 0.190 wind

in which evaporation is expressed as rate (cc./-hr.); v.p.d. as the vapor pressure difference (mm. Hg.); and wind (m.p.h.).

The negative value, −0.18 cc., results from the relationship of normally occurring, low night water losses to comparatively high deficits being measured within the shelters. Plots of these night values, all occurring in the lower portion of the diagram, depress the regression trend to produce a negative value at the ordinate. This lack of correspondence in most night values is due apparently to retarded cooling within the shelter, and to characteristic instrument lag. In comparison, cooling was probably more rapid, as well as greater, at bulb surfaces, causing the sharp reductions in evaporation.

Rapid cooling effects resulting in condensation on bulb surfaces were observed on still nights, particularly in the open site. Here, the inversion effect was apparently more pronounced than in the grove station. In the latter, the rise of warm air was thought to be retarded by the canopy. As a consequence, nocturnal evaporation stress in the grove possibly would be greater.

Table I indicates that the average night evaporation rate was 0.18 cc. in the grove and 0.11 cc., or 39 per cent less, in the open site. Similarly, the independent factors, v.p.d. and wind, were also less in the latter station. These comparisons are in contrast to the daytime effects of the forest canopy on the atmospheric environment as the data indicate. Morning and afternoon readings of all variables were less under the forest canopy.

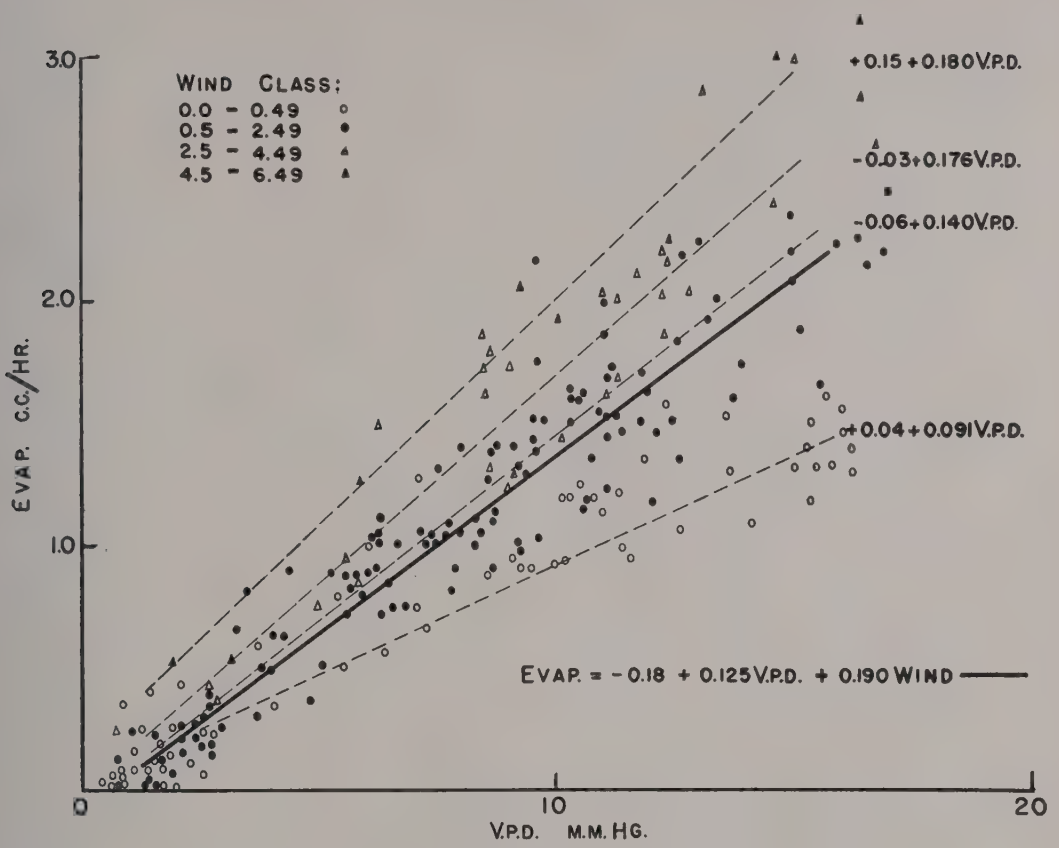

FIG. 1. Scatter diagram of actual data showing relationship of evaporation rate to the v.p.d. and air movement. The multiple regression, including all wind classes, is indicated by the heavy, solid line; the individual, simple regressions showing ascending trend with increasing air movement by broken lines. Evaporation coefficients as a function of the v.p.d. for each wind class are shown on the right of the plotted values.

TABLE I. *Seasonal means by diurnal periods for open field and forest grove, July-August 1951*

Habitat	Period of day	Evap. cc./hr.	V.p.d. mm. Hg.	Wind mph.
Forest grove	6 PM-6 AM	0.18	2.16	0.86
	6 AM-12 N	0.94	6.53	1.50
	12 N-6 PM	1.14	8.56	1.34
Open field	6 PM-6 AM	0.11	1.85	0.77
	6 AM-12 N	1.33	8.86	1.78
	12 N-6 PM	1.82	11.63	1.77
Difference, Open field greater or less than forest grove (%)	6 PM-6 AM	−38.8	−14.3	−10.4
	6 AM-12 N	+41.5	+35.8	+18.7
	12 N-6 PM	+59.9	+35.9	+32.1

No reason is apparent for the slightly larger night wind value in the grove. Figure 1 shows that most night values fall in the two lowest wind classes. Under these conditions in conjunction with lower temperatures, water losses would be curtailed.

If mean data had been obtained by 24 hour intervals, or longer, these night variations in microclimates of the two habitats would have been possibly obscured by the larger daytime values.

In order to evaluate the independent factors of the equation on the basis of component effects, the data were analyzed statistically. Resultant determinations intending to show the relative influence of atmospheric moisture deficit and wind are presented in Table II.

The correlation coefficient, R^2, expresses the per cent of variance in evaporation rate which is causally related to the independent factor. It is apparent that approximately 72 per cent of the water loss rate from clay bulb atmometers is related to the vapor pressure deficit factor. Wind as a separate factor indicates only limited correlation as was expected. This value is shown as 0.155 in the table. However, when applied in conjunction with the deficit, wind becomes rela-

TABLE II. *Standard error, Se, and measure of correlation, R^2, for evaporation based on estimates of independent components, v.p.d. and wind; the significance of regression differences between wind classes*

Dependent variable	Independent variable	Se (cc. H_2O about mean)	R^2 (% of association)	Significance of regression difference between wind classes
Evap.....	V.p.d. + Wind	0.261	0.873	
Evap.....	V.p.d.	0.387	0.715	
Evap.....	Wind	0.661	0.155	
Evap.....	V.p.d. (0.0-0.49)	0.187	0.901	
Evap.....	V.p.d. (0.5-2.49)	0.214	0.885	P .01
Evap.....	V.p.d. (2.5-4.49)	0.279	0.865	not significant
Evap.....	V.p.d. (4.5-6.49)	0.260	0.930	not significant

tively more significant. As an added component, wind reduces to 13 per cent $(100 - 87)$ the original error of disassociation $(28 = 100 - 72)$. Stated in another way, about 54 per cent $(15/28)$ of the error unexplained by the atmospheric deficit is resolved by the factor of air movement. The remaining unexplained variation could possibly be reduced further by measurement of the critical surface temperature with a thermocouple.

Preliminary inspection of the plotted values (Fig. 1) indicated that a series of wind classes probably existed in the mass data. These classes as defined are shown in the legend, the values for which are designated by symbol. It seems apparent that the general trend of evaporation rate rises with increase in wind velocity. Differences in water loss between the several velocity classes become greater under increasing moisture deficits, indicating that wind effectiveness increases with vapor pressure gradients. This conclusion may be drawn only for the range of the data obtained. The velocities at which evaporation rates presumably would begin to diminish for different deficits were not indicated within the range of physical measurements obtained. Graph data presented by Turnage and Shreve (1939) indicate that a leveling in evaporation rate does occur at certain wind velocities for different degrees of aridity.

Correlation values for evaporation and v.p.d. segregated by wind classes are increased from 20 to 30 per cent over the original 0.715 for mass data (Table II). Resultant increases in R^2 values due to segregation of wind data should be expected if wind is a source of variation in evaporation. The higher correlations corroborate the relative importance of wind as a component factor. The calculation of separate coefficients for each wind class (Fig. 1) also indicates a rising rate of evaporation with increase in velocity. The greatest increase in evaporation coefficients as a function of the deficit occurred between the two initial wind populations. This difference was highly significant; however, differences were not significant between the higher wind groups (Table II). This may indicate that for the range of deficits measured, wind is probably most effective at the initial velocities. Beyond this point, the effect on evaporation rate becomes less noticeable. Additional data are needed for velocities exceeding those in the present data in order to make the results more conclusive. As stated previously, no mean velocity was obtained under field conditions which exceeded 7.1 m.p.h. The average velocity for the study was 1.48 m.p.h.

Within the range of field conditions measured, a linear characteristic is indicated for evaporation rate as a function of v.p.d. for the several wind classes. In still air, rate of water loss is regulated by the diffusion gradient, here approximated by atmospheric measurements. With wind, vapor accumulation near the surface is removed, thus increasing the rate of evaporation. It is likely that the greatest variation between the actual water loss potential and the v.p.d. value would occur during windless periods. Under these conditions, the respective microenvironments of the bulb and sheltered instrument would tend to be more dissimilar than when a mixing of air occurred. This may explain partially why most of the v.p.d. values measured on still nights are high in relation to actual water losses. Nonetheless, considering the net trend established by all diurnal periods, the v.p.d. showed an unexpectedly high correlation to evaporation. Its use as an aridity index, however, is perhaps most safely applied to daytime conditions when positive evaporation stresses are most pronounced. Under conditions approaching condensation, as when temperatures of the vaporating surface become much lower than those of the atmosphere, the v.p.d. is unreliable. Under these conditions, a vapor gradient from air-to-evaporating surface may occur, even though the former has the lower humidity. The atmospheric deficit would indicate an evaporation potential, when actually, condensation may be occurring.

SUMMARY

1. An evaporation study was conducted for a five-week period in July and August, 1951, and for two weeks in August, 1952. The principal purpose of the study was to evaluate by analysis the importance of the vapor pressure deficit and wind as factors in evaporation rate. Two adjacent stations with similar aspect were selected, one an open bluegrass field, the other a small forest grove. Livingston-type atmometers were used, with measurements being made for the periods ending at 6 a.m., 12 noon, and 6 p.m. Psychro-

metric and wind data for these intervals were obtained by recording instruments.

2. Based on the data for the two seasons, a multiple regression was determined for evaporation rate as a function of the v.p.d. and wind velocity.

3. The correlation of evaporation rate to the v.p.d. exceeded 70 per cent. Wind as a separate factor showed only limited correlation. As a component factor, however, it decreased variance in evaporation unrelated to v.p.d. by 54 per cent.

4. Increasing wind velocities, in the range studied, increased the rate of evaporation, the v.p.d. remaining constant. Wind effectiveness was most pronounced in the initial velocity classes, and diminished as air movement increased.

5. Under conditions approaching condensation, as on still nights when temperatures of evaporating surfaces dropped considerably below those of the air, the v.p.d. was an unreliable index of the evaporation potential.

6. Mean evaporation rates for the morning and afternoon periods were respectively 42 and 60 per cent greater in the open field compared to the forest grove. Similarly, v.p.d. and air movement were also greater. Furthermore, no average wind speeds exceeding four miles per hour were recorded in the grove, whereas over 10 per cent of all observations exceeded this velocity in the open. Conversely, night values for all variables, evaporation rate, v.p.d., and wind, were greater in the grove station. Moderating influences of the forest canopy on the microclimate were apparent.

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MARINE FISHES IN FRESH AND BRACKISH WATERS OF VIRGINIA RIVERS[1]

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In the fresh and brackish waters of the James, Chickahominy, Pamunkey, Mattaponi and Rappahannock rivers in Virginia, 18 species of marine fishes (exclusive of anadromous and catadromous forms) have been collected. Gunter's (1942) exhaustive survey of the occurrence of Atlantic coast marine fishes in fresh water is here amplified for the most important tidal rivers of Virginia.

Since 1949 intensive collecting has been done in brackish and tidal fresh waters of the Pamunkey and Rappahannock rivers, and numerous collections have been made in the James, Chickahominy, and Mattaponi. The samples include 261 collected by minnow seine, 39 by gill net, 12 by rotenone and 81 by surface trawl (Massmann, Ladd, and McCutcheon 1952). In addition more than 845 plankton net samples, using nets one meter in diameter at the mouth, were made both

[1] Contributions from the Virginia Fisheries Laboratory, No. 47.

at the surface and near the bottom. Collections were made from February to October inclusive, but summer collecting was most intensive. For convenience in summarizing the data, the rivers were divided into five-mile intervals, and all collections in each interval were lumped. No marine fishes have been taken in these rivers and their tributary creeks beyond the limits of tidal excursion.

Since the boundary of brackish and fresh waters oscillates with the tide, moving one or two miles upstream with the flood and one or two miles downstream with the ebb, the average location of this boundary has been used. Extremes in rainfall, drought, and wind may displace this boundary by considerable distances. Collections were not made under these extreme conditions.

The marine species taken in brackish (salinity of five parts per thousand or less) and fresh water are listed in Figure 1. The greatest distance in nautical miles upriver at which marine fishes were captured, the number of rivers in which they have been collected, and the number of species taken at varying distances upriver from brackish water are indicated. The distances upriver from Chesapeake Bay to the average location of the boundary of brackish and fresh water and the river length from this boundary to the head of the tide are listed in Table I.

TABLE I. *The distance upriver from Chesapeake Bay to the location of the average boundary between brackish and fresh water, and the length of the tidal freshwater section for the five major tidal rivers in Virginia.*

River	Distance upriver from Chesapeake Bay to location of average boundary between brackish and fresh water (Nautical miles)	Distance from the average boundary between fresh and brackish water to the head of tidal water (Nautical miles)
James	30	55
Chickahominy	..*	20
Pamunkey	30	40
Mattaponi	30	35
Rappahannock	45	50

*A tributary of the James River.

ANNOTATED LIST OF MARINE FISHES

Brevoortia tyrannus (Latrobe), Menhaden.—Found in all five rivers, young menhaden were abundant in fresh waters of the Rappahannock River, where they were captured 35 miles upriver from brackish water. Adults have not been collected in fresh waters.

Anchoa mitchilli mitchilli (Valenciennes), Mitchill's anchovy.—Numerous in all rivers, some anchovies were captured 40 miles upstream from brackish water. Adults, young, and postlarvae were abundant in surface trawl collections and some were taken by seine.

Anchoa hepsetus hepsetus (Bonaterre), Anchovy.—A single specimen was obtained from brackish waters in the Mattaponi River.

Strongylura marina (Walbaum), Atlantic needlefish.—Commonly found in fresh waters, several needlefish were collected 40 miles upstream from brackish water. Two were taken at the head of the tide in the Pamunkey River. Most of the specimens were adults. It is possible that the species sometimes spawns in fresh water, for eggs were running freely from a female taken in the Chickahominy River 10 miles above brackish water on May 9, 1952. A specimen 23 mm. in length was caught in the Pamunkey.

Fundulus majalis (Walbaum), Striped killifish.—A few striped killifish were found in brackish waters of the Pamunkey River. The species is abundant in more saline waters nearer the river mouths.

Fundulus heteroclitus macrolepidotus (Walbaum), Mummichog.—The mummichog was often captured in fresh water in the James and Rappahannock rivers and occasionally taken in the Pamunkey and Mattaponi. Adults were taken 45 miles upstream from brackish water. Numbers were observed spawning in a shallow cove 35 miles upriver from brackish water in the Rappahannock River, August 2, 1951.

Cyprinodon variegatus (Lacépède), Variegated minnow.—Many were captured in a tidal creek of the Rappahannock River where the salinity was less than five parts per thousand.

Menidia menidia (Linnaeus), Atlantic silverside.—Small numbers of adult Atlantic silversides were taken as far as 30 miles upriver from brackish water in the James, Rappahannock, and Pamunkey rivers. In salt water near the river mouths this species is common.

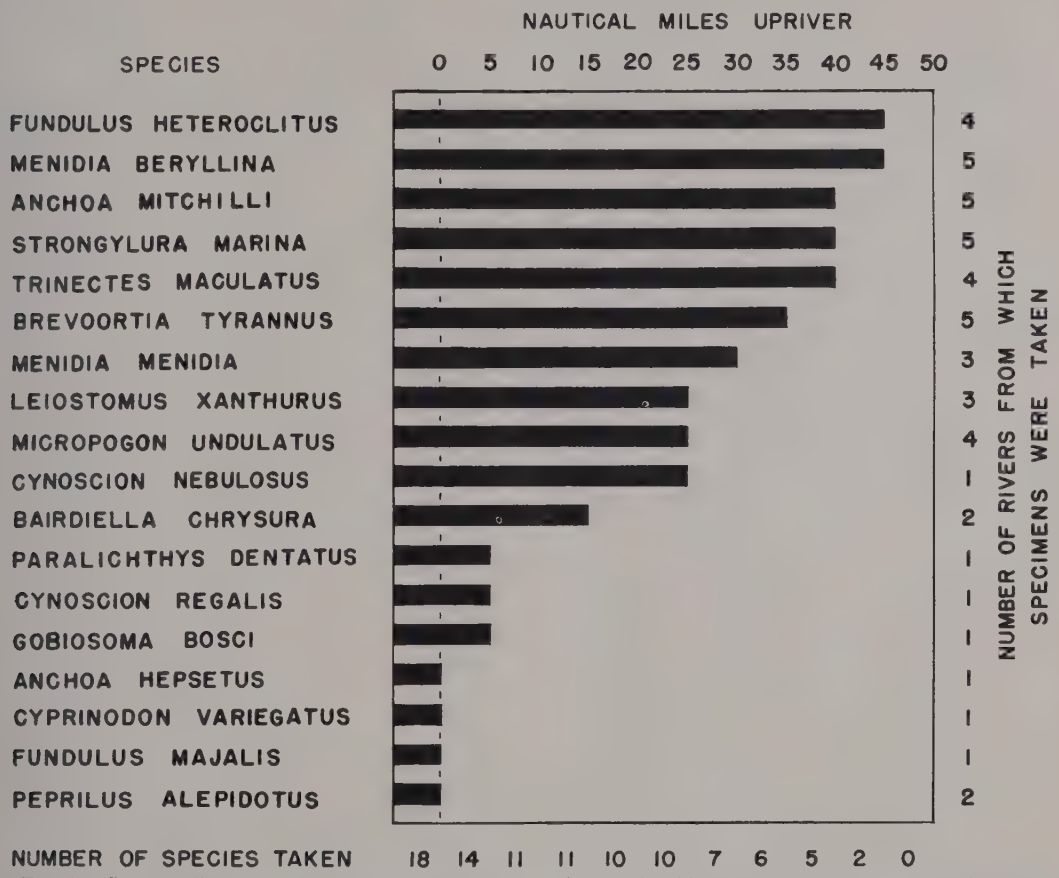
NAUTICAL MILES UPRIVER
SPECIES
0 5 10 15 20 25 30 35 40 45 50
FUNDULUS HETEROCLITUS 4
MENIDIA BERYLLINA 5
ANCHOA MITCHILLI 5
STRONGYLURA MARINA 5
TRINECTES MACULATUS 4
BREVOORTIA TYRANNUS 5
MENIDIA MENIDIA 3
LEIOSTOMUS XANTHURUS 3
MICROPOGON UNDULATUS 4
CYNOSCION NEBULOSUS 1
BAIRDIELLA CHRYSURA 2
PARALICHTHYS DENTATUS 1
CYNOSCION REGALIS 1
GOBIOSOMA BOSCI 1
ANCHOA HEPSETUS 1
CYPRINODON VARIEGATUS 1
FUNDULUS MAJALIS 1
PEPRILUS ALEPIDOTUS 2
NUMBER OF RIVERS FROM WHICH SPECIMENS WERE TAKEN
NUMBER OF SPECIES TAKEN 18 14 11 11 10 10 7 6 5 2 0

FIG. 1. Greatest distance upriver from the average boundary of brackish and fresh waters that marine fishes have been taken in five Virginia rivers. The boundary is shown by a vertical, dashed line. The left hand margin represents a mean salinity of 5 parts per thousand.

Menidia beryllina (Cope), Glassy silverside.—Generally considered a marine species, glassy silversides were collected as much as 45 miles upriver from brackish water in the Rappahannock River. Adults and young were common in the five rivers. Glassy silversides appear to be more abundant in fresh, tidal water than in salt water downstream.

Peprilus alepidotus (Linnaeus), Harvestfish.—Small numbers of harvestfish were trawled in brackish waters of the Pamunkey and Mattaponi rivers.

Cynoscion regalis (Bloch and Schneider), Gray squeteague.—Small specimens were trawled five miles above brackish water in the Pamunkey River.

Cynoscion nebulosus (Cuvier and Valenciennes), Spotted squeteague.—Not listed by Gunter (1942) in fresh water, young spotted squeteague were obtained in surface trawl hauls from fresh water in the Rappahannock River. Of eleven specimens captured, two were taken 25 miles above brackish water.

Bairdiella chrysura (Lacépède), Silver perch.—A few young silver perch have been taken in the Pamunkey and Rappahannock rivers at distances up to 15 miles above brackish waters.

Leiostomus xanthurus (Lacépède), Spot.—Young have been captured in the Pamunkey, Mattaponi, and Rappahannock rivers. Although spot were more abundant near brackish waters, a few were found 25 miles farther upstream. Young spot collected in salt water (salinity 20 parts per thousand) were maintained in a laboratory tank of fresh tap water for a period of one month with no apparent ill effects.

Micropogon undulatus (Linnaeus), Atlantic croaker.—Small croakers were found in four riv-

ers during the spring months. Three small individuals less than 30 mm. in length were found 25 miles above brackish waters, but most were obtained closer to the sea. Recent work by Dexter Haven of the Virginia Fisheries Laboratory is establishing the importance of tidal estuaries as a croaker nursery ground.

Gobiosoma bosci (Lacépède), Naked goby.—Several gobies were collected in minnow seine samples up to five miles above brackish water in the Pamunkey River.

Paralichthys dentatus (Linnaeus), Summer flounder.—A single specimen was seined in the Pamunkey River five miles upriver from brackish water.

Trinectes maculatus (Bloch and Schneider), Hogchoker.—Hogchokers were common in the James, Pamunkey, Mattaponi, and Rappahannock rivers. Some were found 40 miles beyond brackish water. These fish were mostly small.

Summary and Conclusions

The transition from salt to fresh water in Virginia tidal estuaries is not abrupt. It is possible that very slight amounts of salt of marine origin may be present up to the head of tide, but these amounts become increasingly difficult to detect by conventional methods at increasing distances upstream. Small amounts of salt water may become detached from the main body of salt water and moved upriver by eddies (Donald W. Pritchard, personal communication). A series of salinity samples from the "fresh" tidal waters titrated with silver nitrate has indicated that salinities did not decline steadily until they reached the normal salt content of fresh water, but seemed to show small erratic differences. Most of the salinities reported here were obtained by hydrometer readings, which cannot be considered accurate below one part per thousand. It is possible, therefore, that slight traces of salt may be responsible for the ability of some marine species to survive in waters considered to be "fresh."

Some marine species are able to adjust themselves to life in "fresh" water. The degree of adjustment varies among the different species and age groups. In the five Virginia rivers considered, the marine fishes may be divided into three general groups: (1) fishes commonly found in fresh water both as young and adults, including mummichog, glassy silverside, Atlantic needlefish, and Mitchill's anchovy; (2) fishes that occur in fresh water usually only as young, including hogchoker, menhaden, spot, Atlantic croaker, silver perch, and gray squeteague; (3) fishes rarely taken either as young or adults, including spotted squeteague, winter flounder, Atlantic silverside, and naked goby. To this last category might be added the fourspine stickleback, *Apeltes quadracus* (Mitchill), reported by Raney (1950) in fresh waters of the Rappahannock River.

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EVIDENCE FOR THE RECENT ENLARGEMENT OF THE "BAY" LAKES OF NORTH CAROLINA[1]

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The almost inevitable fate of most lakes is extinction through the accumulation of autochthonous and allochthonous sediments and the lowering of the outlet level, if the lake has an outlet, with advancement in the physiographic cycle. Hundreds, and probably thousands, of the lakes owing their origin to the most recent ice sheet have become obliterated as basins, and a much greater proportion of the basins dating from earlier ice sheets have similarly been affected. Lake succession is generally conceived to be a unidirectional process, except in arid regions where the water surface depends largely on the magnitude of interior basin drainage. The latter basins can again contain lakes when conditions become suitable, whereas the glacial basins that have become filled with

[1] Contribution No. 529 from the Department of Zoology, Indiana University, Bloomington, Indiana.

sediments can never again contain lakes, regardless of how much surface water is present.

Because of this ephemeral nature of lakes, it is most interesting when small bodies of water are discovered which have been in existence for a long period of time. Such are the lakes of the Carolina "bays" in Bladen County, North Carolina. Although none of these has a water depth greater than 12 feet, and nowhere do the nonarenaceous sediments extend deeper than 25 feet below water level, the basins have been in existence at least since early Wisconsin time (Frey 1953). The known rates of sedimentation have been as low as one inch in 730 years for the post-Wisconsin sediments at site Si-25 in Singletary Lake (Frey 1951).

Not only has the filling process been extremely slow, but there is evidence that it has not been harmonic: the lake areas have alternately contracted and expanded, even within the confines of their present sand rims. The lakes at present are in a phase of modest expansion.

General Description of the "Bay" Lakes

The bay lakes lie in oval basins, each surrounded more or less by a sandy rim, which is highest toward the east and southeast. The lake itself tends to be completely surrounded by organic soil (peat) except possibly at the southeast end where the lake comes closest to the sand rim. Along the eastern and southern quarters of the shore there tends to be a well-developed terrace of equilibrium, resulting in the shallowest littoral water anywhere in the lake. Along the northwestern shore, where, according to the aerial photographs, filling seems to have progressed most rapidly (Figure 1), the water is deepest, sometimes being four feet or more in depth right at the shoreline. The shore material in these localities is peat, bound together with roots of various kinds of bay shrubs. All of these morphometric features are described in detail for the various lakes in an earlier paper (Frey 1949).

Cypresses (*Taxodium ascendens* Brongn.) occur in all the lakes at varying distances from shore in varying depths of water. Sometimes these cypresses occur in rather dense and apparently homogeneous stands, as at the south end of White Lake and the southeast end of Lake Waccamaw, but more frequently they are scattered and heterogeneous as to size. Occasional cypresses are found even along the northwest shore in water up to four feet deep. The lake sediments at these latter locations are entirely organic.

Methods

Several important aspects of this paper are based upon the ages of cypresses occurring in the lakes. These cypresses were sampled with a Djos 12-inch increment borer, kindly made available for this work by Mr. Rufus Page of the Bladen County State Forest. The very small cypresses in Lake Waccamaw were simply cut below water level with a machete, and suitable lengths of the trees were saved for analysis.

In the laboratory, the cores were prepared for examination according to the procedure described by Hawley (1941), which is apparently more or less standard in dendrochronology laboratories (Glock 1937). The cores were examined with a stereoscopic microscope at a magnification of 9 diameters.

Where the growth of the cypresses was rapid there was often a morphological change in the wood structure about ⅔ of the way through the growth increment of the particular year, which resembled the annual ring quite closely. Under conditions of rapid growth, these "mid-lines" could be distinguished from the true year marks quite readily. Where the growth was slower, however, as was the case in most cores of this series, such accessory marks if they occurred could not easily be separated from the true annuli by the gross methods employed. Just from the appearance of the cores, the author is inclined to believe that double rings did not form during years of very slow growth. An allowance of 10 per cent error should adequately take care of all such instances. In the several instances where two or three cores were obtained from the same tree, the age determinations usually differed by less than five per cent. Accuracy greater than this is not necessary for the purposes of the present study.

For those interested in dendrochronology, it might be pointed out that the cores of these lake cypresses do not seem to be favorable material for establishing a dendrochronology. There is a great individual variation from one cypress to another, and of course the situation is complicated by the expansion of the base of the trees. It is conceivable that the annual growth increment is governed primarily by hydrologic conditions rather than meteorologic, without their being too close a dependence of the hydrologic conditions on the meteorologic.

Argument

If it is agreed that cypresses can become established only on exposed surfaces (Demaree 1932, Wells 1942, Hall, *et al.* 1946), then the occurrence of these trees away from shore means that either: 1) the lake level at some time was low

FIG. 1. Aerial photograph of Singletary Lake, N. C., showing the typical oval shape and orientation of the Carolina bays. The dark area between the water and the white sand rim represents organic soil with its dense cover of vegetation. (USDA, Production and Marketing Administration.)

enough to permit the cypresses to become established in their present location, or 2) the cypresses were associated with a previous shore line but by subsequent erosion of the surrounding soil they were eventually isolated from the shore. Both processes have undoubtedly occurred.

Buell (1939) considered that the pond cypress is the principal pioneer in this particular hydrosere, becoming established during the low water levels of extreme dry seasons. The expanded bases and knees of established trees then form sites for the development of islands of typical "bay" shrubs and trees. These expand, coalesce, and form a solid organic surface, thereby obliterating the previously existing water area. Aiding in this process are the root systems and stolons of the "bay" shrubs growing along shore.

Although the pond cypress very likely is the first pioneer in this succession, the "islands" now present in the lakes represent portions of an original shore which have not yet been completely destroyed by erosion, rather than more advanced stages in the succession as described by Buell. Furthermore, the cypresses themselves although the pioneer plant in this hydrosere, are not advancing the succession under present conditions.

Establishment of Cypresses on Exposed Lake Bottom at Low Water Levels

The present morphometry of the lake basins is such that a lowering of the water level by about a foot, as commonly occurs each year, does not expose any appreciable area of the lake bottom. A further lowering, however, first exposes bottom at the southeast end, where the extensive and shallow littoral shelf occurs. One might expect, therefore, that if cypresses were to become established on the lake bottom during periods of low water, they would be most likely to occur in this general area. There is evidence that this has occurred in White Lake and Waccamaw, and probably in Singletary Lake as well.

a. White Lake

Along the south shore of White Lake there is a rather dense stand of small cypresses extending out approximately 70 feet from shore, the outermost trees being in about 20 inches of water at average conditions (Figure 2). Because of the small diameter of the trees, ranging from about three to seven inches above the markedly expanded base typical of cypresses growing in water, one might be inclined to consider them fairly young trees. Cores taken with an increment borer, however, show that the age of these trees is remarkably uniform, the actual counts ranging from 125 to 158 years (Table I). Considering the close spacing of the annual rings, with an error in age determination of at least 10 per cent not unreasonable, particularly in the smallest trees, and the time required for the trees to reach the height at which the cores were collected, the actual age of these trees may well lie between 160 and 180 years. This would place their origin during or shortly after the Revolutionary period.

There is evidence that someone, possibly Col. William Bartram, operated a sawmill on White Lake during the decade or two after 1770. A channel was cut through the sand rim at the southeast end of the lake, and supposedly the lake level was lowered two feet during the logging activities.

Fig. 2. Part of the 70-foot wide homogeneous stand of cypresses at the south end of White Lake. These trees vary in diameter from 3 to 7 inches above their expanded bases.

The millrace is still evident at Melvin's Resort, and although the channel has been dry for many years, there are some cypresses present. The age of one of the three cypresses sampled (No. 13 in Table I) was about 160 years in each of two cores, or in other words the same as the cypresses in the lake. Since cypresses could not possibly become established on the xeric sand rim except where the water relations are artificially altered as in the sawmill channel, the age of this channel and hence of the sawmill extends back to the late 1700's. This is the time of Col. William Bartram, so that he may well have operated the sawmill. A map by Price and Strothers dated 1808 (reproduced in Harper 1942) designates the lake under discussion as Bartram's Lake.

The presence of stumps of logged cypresses at the northwest end of the lake about two feet below the present water level, and the presence of this extensive population of small cypresses at the southeast end in up to two feet of water, demonstrate that the lake level probably was lowered about two feet during these logging operations. Certainly there is little doubt that this stand of cypresses derives from this period and that they became established on exposed lake bottom.

It is noteworthy, however, that in this relatively long span of time no "islands" of bay vegetation have begun to form around the bases of the cypresses and there is no accumulation of peat; rather the bottom is entirely sand, as it is everywhere else on the littoral shelf. These cypresses are being thinned out gradually by natural processes, as evidenced by stumps and scraggly, weak individuals. Succession is not progressing but retrogressing. Conditions were initially favorable for establishment of the stand, but subsequently have not been favorable for the growth and further development of the sere. It is believed the factor primarily responsible for this condition is the wave action at the southeast end. Hence, the force which produces the conditions (the littoral shelf) most suitable for cypresses to become established during low water stages also makes it difficult for the trees to thrive after becoming established.

b. Lake Waccamaw

On the shallow littoral shelf at the southeast end of Waccamaw, likewise, there is a dense stand of cypresses which has become established at low

TABLE I. *Age and rate of growth of cypresses from the bay lakes in relation to depth of water and distance from shore*

Lake and date	Cypress number	Distance from shore (feet)	Depth of water (inches)	Height of core above bottom (inches)	Diameter at height sampled (inches)	Length of core (mm.)	Counted annual rings	Annual rings per mm.	Estimated age at height sampled
White	1	70	20	49	5	47.4	142	3.0	145
24 Aug. 48	2	70	20	59	6	69.7	153	2.2	158
	3	70	19	58	6	61.2	139	2.3	142
	4	30	14	55	3¾	33.8	127	3.8	127
	5	30	14	56	4	44.2	144	3.3	144
	6	12	11	58	5¾	83.3	146	1.8	148
	7	8	14	61	7	80.0	138	1.7	138
	8	4	8	60	5¾	64.3	136	2.1	140
	9	9	8	52	3¼	27.7	129	4.7	129
	10	1	5	96	11	95.0	389	4.1	>500
	11	8	11	53	2¾	27.6	125	4.5	125
	12	In millrace		61	11	111.0	103	0.9	106
	13	" "		61	9	100.0	160	1.6	160
	14	" "		61	7½	75.4	47	0.6	50
Singletary	15	80	13	67	9½	66.5	328	4.9	>500
24 Aug. 48	16	70	13	65	9	92.0	374	4.1	374
	17	80	17	67	11	~ 97.0	405	4.2	>500
	18	100	29	63	11	57.8	212	3.7	>500
	19	20	48	126	11	117.6	328	2.8	333
	20	15	46	122	14	129.7	317	2.4	>400
	21	30	46	108	23	170.9	304	1.8	>450
	22	12	46	118	13	~175.0	424	2.4	430
	23	25	48	100	13	127.6	271	2.1	277
	24	50	48	99	15	99.0	133	1.3	~250
	25	120	27	71	13	~140.0	458	3.3	491
Jones	26	75	12	78	12	82.6	400	4.8	>650 ?
15 Aug. 48	27	75	12	60	12	116.3	417	3.6	435
	28	75	14	56	12	137.3	530	3.9	538
Salters	29	15	12	60	14	132.8	96	0.7	99
23 Aug. 48	30	10	12	60	11	68.3	105	1.5	130
	31	30	14	60	10	122.7	66	0.5	68

water levels. These trees are much younger than those in White Lake. The diameter of 22 trees at the height sampled (about 12 to 14 inches, which is also the depth of water) varied from 9 to 24 mm., with a mean of 15 mm. The apparent age of these trees as of 1949, based on a study of four cross sections from each tree, ranged from 5 to 15 years, with a mean of 11 years. There is a greater frequency toward the upper end of this age range. The cross sections of these young trees demonstrate clearly some of the errors that can readily occur in aging trees, apart from correctly recognizing and counting the annual rings. Some of the annual rings on various cross sections were present only part way around, and in other instances an annulus present on one cross section might be completely lacking on another cross section taken only an inch or two farther up or down the stem. These are problems that confront all dendrochronologists.

Considering the vertical growth of these trees to have been about three inches per year, most of the trees became established during the period 1931 to 1936, with minor amounts of seeding as late as 1939. It is known that the water level of Lake Waccamaw fluctuated greatly during this period. Only a makeshift dam was at the outlet to help control the minimum water level, and this dam washed out at least once during the period. Since the construction of a concrete dam at the outlet the annual fluctation in water level has been less, and there has been no further seeding of cypresses on the littoral shelf.

c. Singletary Lake

Singletary Lake is the only one of the bay lakes with large cypresses at any appreciable distance from shore at the southeast end of the lake (Figure 3). Trees number 15, 16, and 17 in Table I are from this region. Only number 16 yielded a complete core, with an age of 374 years. Trees 15 and 17 had rotten centers so that complete cores were impossible to obtain. Assuming the rate of growth was the same throughout as in the partial cores obtained, the total age of these trees would be considerably greater than 400 years, even al-

lowing a 10 or 20 per cent error in counting the annuli.

If these trees became established when the lake bottom in this region was exposed, such exposure occurred a very long time ago and apparently has not been repeated within the past few hundred years, at least with the survival of any cypresses that may have become established. The cypresses present may be the remnants of much more extensive stands, such as those in White Lake and Waccamaw. Since, however, it is likely that these cypresses differ considerably in age they may be erosional remnants of the type to be described presently.

Again it should be noted that there is no tendency for any of these trees, in spite of their great age, to serve as foci for formation of islands of bay shrubs or for accumulations of peat. The bottom surrounding these trees is entirely sand.

Isolation of Cypresses from Shore by Erosion

On the other hand there is considerable evidence that many of the cypresses in the lakes were originally out of the water, and have since been isolated from the shore by erosional processes. The most direct evidence for this is the small "islands" of shrubs around the bases of some of the cypresses, which Buell regarded as evidence of progression in the succession, rather than the reverse as believed in the present paper.

One of these "islands" is shown in Figures 4 and 5. It consists of a cypress tree along the northeast shore of Jones Lake surrounded by a dense growth of *Cyrilla* and *Clethra*. A second live cypress is seen extending obliquely from the left side of this island, and a dead cypress projects from the right. The evidence for regarding this "island" as an outpost of the former shore is the following.

1. Cypresses growing in water tend to develop greatly *swollen bases,* such as those shown in Figures 3 and 6, which have obviously been in the water for a long time. Cypresses growing out of the water do not develop the swollen base to anywhere near this degree. The cypresses in this clump have only a slightly swollen base (hidden by the shrubs).

2. The cypresses in the lake tend to have two *horizontal marks* on their bases at distances above the water level which are the same for all the trees (Figure 6). These marks are more prominent on the lakeward side of the tree than on the shoreward side. They do not occur on the trees growing on shore. The author's interpretation of these particular marks is that they are abrasion features formed during two particular high

Fig. 3. Ancient cypresses on the littoral shelf at the southeast end of Singletary Lake. Note the several pines growing at the edge of the water apparently being cut away from the shore by wave action.

FIG. 4. A cypress "island" in Jones Lake about 15 feet from shore.

water periods. Because high water occurs in the early part of the year, it is believed these marks possibly resulted from fractured ice moved by a strong wind. Regardless of their origin, however, they occur at corresponding levels on trees in the water but do not occur on trees out of the water. The cypresses in this island (and the cypresses in similar islands elsewhere) do not have these abrasion marks on their bases.

3. The general aspect of the tangled mass of roots around the base of this island is one of *degradation* rather than aggradation. Many of the roots are bare without any soil around them at all. The roots in the water away from the island belong to the two living cypresses in this island, and are similar in aspect to the roots surrounding the other cypresses in the lakes (Figure 6). Normally these roots are under water; the photographs were taken at such an extreme water stage that sponges on these roots, for example, were three inches *above* the water surface at this time

FIG. 5. Closer view of the base of the cypress "island" in Figure 4, showing the exposed roots of the cypresses and bay shrubs and the general aspect of degradation.

(August 15, 1948). No appreciable portion of the littoral shelf was exposed even at this low water level.

4. The great tangle of *cypress roots* in the water may be another indication that erosion has occurred. Cypresses ordinarily form an extensive horizontal root system beneath the ground surface. Photographs in the paper by Brown (1943) show the soil washed away from around the roots of cypress trees, giving an aspect somewhat similar to that around the island. By contrast, the cypresses at the south end of White Lake (Figure 2), which are known with some certainty to have been established at a low water level, do not have similar extensive root systems in the water.

This particular island was 15 feet from the present shoreline. Other islands are at a somewhat greater distance, and a few are barely separated from the shore. The latter applies to cypress No. 10 from the south end of White Lake. It should be mentioned that these accumulations of shrubs around the bases of the trees are not common. Usually the trees are completely isolated from any other vegetation except the *Sphagnum* and *Fontinalis* on their roots in the water, or the occasional liverworts on their boles.

OTHER EVIDENCE FOR SHORELINE EROSION

Realizing that erosion has occurred, there are some features of these lakes that can be best explained on the basis of such erosion.

1. Along the eastern shore of Jones Lake just north of the outlet there are three small scallops or indentations of the shoreline. Paralleling the two upper scallops almost exactly and at a distance of approximately 75 feet from shore is a row of ancient cypresses, about 15 in number. A considerable number of these cypresses is shown in Figure 6. Each of the trees is surrounded by an extensive root system in the water (exposed in the photograph because of the extremely low

FIG. 6. Part of the row of cypresses paralleling shore in Jones Lake. The abrasion marks on the expanded bases are readily visible, as are also the extensive systems of roots in the water, here exposed at very low water level.

water level). The butts of all these trees are greatly expanded, but there are almost no "knees" of the type usually occurring in aquatic cypresses. It will be observed in Figure 6 that there is no island development around these trees, even though such development ought to be encouraged rather than discouraged by these extensive aquatic root systems.

The question is, has this row of cypresses paralleling the shore originated through establishment at a very low water level, or has it originated through isolation by erosion from a previous shoreline? The evidence seems to favor the latter view.

Borings obtained from three of these trees (numbers 26-28 in Table I) reveal that although all the trees are very old, they are probably not the same age. The cores for trees 27 and 28 were reasonably complete, so that depending on the accuracy with which the annual rings were interpreted and counted, the ages should be roughly the order of magnitude shown in Table I, with the addition of the number of years necessary for each tree to reach a height of about five feet above the present ground level. Cypress number 26, however, had a hollow center, necessitating an extrapolation by more than a third of the counted number of annuli to obtain the estimated total age.

Granting that these trees are not the same age but differ by perhaps 50 to 200 years, their present linear arrangement paralleling the shore is more logically the result of erosion of a previous shoreline, where conceivably cypresses could become established almost every year, than the result of the purely coincidental alignment parallel to shore through establishment over a number of very low water stages occurring within a time span of a couple hundred years.

A further fact opposed to the latter conclusion is that the bottom configuration of the lake while very regular is not so precise that if the lake level were lowered say 2 feet the new shoreline would parallel with any exactness the minor indentations of the present shoreline.

2. The south and southeast shores of Black Lake are very irregular, with many narrow tongues of cypresses and bay vegetation extending out from shore, forming numerous small embayments of the lake measuring from 50 to 100 or 150 feet across. The vegetation in these small peninsulas is growing in organic soil which extends above the water level, and again the over-all aspect is one of degradation (as in Figure 5). In

addition there are quite a few cypresses completely isolated from shore, with no "islands" of bay shrubs surrounding their expanded bases. It is the author's opinion that these features in Black Lake have resulted from the erosion of a previous shoreline more centrally located than the present one.

3. The occurrence of cypresses in water as deep as four feet along the *northwest* shore of these lakes is difficult to explain except by isolation by erosion from a previous shore. A drop of water level of four feet would be extremely rare in occurrence, and with less extensive lowering of lake levels the cypresses would become established along other shores. As already mentioned, the shallowest water is at the southeast end of these lakes, and the littoral water tends to increase in depth as a function of distance away from the southeast end, both in a clockwise and a counterclockwise direction, reaching its maximum along the northwest end. This statement does not hold true for Waccamaw, because in this lake the organic filled-in portion of the basin at the northwest end has become isolated from the extant lake by deposition of sand. Even so, however, the bottom drops off much more rapidly here than toward the southeast end.

The cypresses were studied more intensively in Singletary Lake than in any of the others. A complete circuit of the lake was made, beginning at the southeast end. It was difficult to locate cypresses without hollow centers or without layers of rotting wood, either of which conditions yielded an incomplete core.

Cypresses 19 to 22 in Table I occurred within a lineal distance of 500 feet along the extreme north shore of the lake. Although these trees are all in water four feet deep, number 19 is definitely younger than the rest. Moreover, number 20 is surrounded by a residual island of bay vegetation and peat, which appears to have been quite recently isolated from the shore. The base of this tree was much less expanded than those of adjacent trees in the water without such an island of shrubs.

Cypress 21 is one of the largest in the lake, and its estimated age was also very great. The largest cypress in the lake, growing along the southwest side in 51 inches of water 80 feet from shore, had a diameter of 27 inches approximately 9 feet above the lake bottom. A satisfactory core could not be obtained, but examination of the fragments indicated as slow a rate of growth as in the other trees of this region.

Cypress 23 and 24 are interesting in that although the trees are growing in four feet of water, their ages are much smaller than those of the cypresses at the north end. Number 23 is particularly interesting in that although 25 feet from the present shore line, the basal portion of the trunk is charred by fire. The present vegetation of the adjacent shore consists of shrubs, and it is inconceivable how even an intense fire in such vegetation could produce charring 25 feet away. Either this cypress was much closer to the shore at the time of the fire, or perhaps it was surrounded by an island of bay shrubs, which has disappeared since the fire. It is extremely doubtful that this tree became established in its present relation to the shoreline as a result of a lowering of the lake level by four feet.

4. It is known to be true for Singletary, Jones, White, and Waccamaw (and presumably for Salters and Black lakes as well) on the basis of reliable testimony that only a short distance below the sand of the littoral shelf particularly along the east and southeast shores are *tree stumps in situ*. The author has observed these personally only in White Lake and Singletary Lake. The species of trees represented are not known, but it is very likely that many of them are cypresses.

Regardless of whether these trees became established at low water levels away from shore or were originally part of shore and then later became isloated by erosion, they provide additional evidence that the successional sequence which bring about encroachment upon and gradual obliteration of the lake area has been retrogressing rather than progressing.

Discussion

Buell's (1939) concept concerning the role of the pond cypress as the pioneer in the hydrosere of these lakes is probably correct, and likewise the accumulation of "islands" of bay shrubs and organic soils around the bases of these trees. On the other hand, there is evidence from the pollen analysis of the sediments of a number of these bays (Frey 1953) that in the filling process accumulation of sediments offshore may have been of relatively greater importance than marginal encroachment of vegetation.

Pollen of all the vegetational components of a region do not turn up in a pollen diagram, at least in frequencies corresponding to the actual occurrence of the plants. One, therefore, must seek out any bits of evidence which seem to indicate trends. In the pollen diagrams from filled-in regions, there seems to be a distinct stratigraphic sequence of peaks of cypress, tupelo (*Nyssa*), *Sphagum,* and composites—*Ilex,* in that order beginning with the post-glacial broadleaf maximum.

It was concluded that this sequence reflected a progressive reduction in duration of hydroperiods. Such a reduction could result from decrease in water depth through accumulation of sediments, decrease in moisture entering the basin (almost entirely direct precipitation), or increase in loss of water from the basin by subsurface leakage and surface drainage.

For reasons as yet unknown, the rate of sedimentation in the extant bay lakes has been extremely slow, so that the hydroperiod of the offshore areas is continuous, and the hydroperiod even of the littoral areas is almost continuous. Those cypresses which do become established in the latter areas during the very infrequent interruptions of the hydroperiod find conditions difficult for maintaining themselves (as evidenced by very slow growth rates) and do not provide a satisfactory base for development of more complex communities. Moreover, at times such as the present, their role is minimized even further by the actual reversal of successional trends through erosion of the organic shores. It is interesting that Wells and Boyce (153) have recently arrived at the same conclusion regarding erosion, independently of the present author.

If peripheral expansion of the lake areas is occurring under present conditions, there is no reason to believe that it may not also have occurred at various times in the past when conditions were suitable, and very likely at greater rates than at present. The author conceives of these lakes as having undergone an areal expansion and contraction at various times during their ontogeny. This concept has an important bearing on two matters relating to the final understanding of the origin and ontogeny of these basins.

First, it has pointed out by the author (Frey 1953) that although the regional pollen succession was definite and readily capable of correlation from one basin to another, yet there were instances (particularly in Little Singletary Lake and White Lake) when the typical succession of pollen types was somewhat masked and obscured by considerable frequencies of "extraneous" pollen grains. Such "mixing" is believed to have resulted from phases of erosion similar to the present at various times in the past. Erosion brings about a redistribution over the lake bottom of pollens and spores deposited during earlier phases of contraction of lake area (or prolonged periods of lowered lake level). It is necessary, therefore, to be aware of this phenomenon and be alert for vidence of it in interpreting pollen diagrams from the Carolina bays.

Second, adherents of the meteoric hypothesis as to the origin of these oval depressions in the Atlantic Coastal Plain conceive of the process of basin filling as being undirectional: the basins were formed essentially in their present shapes and orientation, and these have persisted unaltered to the present with the exception of the accumulation of sediments (Prouty 1952). Instances where the highly regular outline of one bay is cut into by that of another bay, in the same way as during a lunar eclipse the earth's shadow appears to be taking a bite out of the moon, are explained by two meteorites striking the earth successively within a short distance of one another. The meteorite striking last would produce the basin having the completely regular outline which would appear to be taking a "bite" out of the slightly earlier basin. A contrary view that such intersections of bays may have resulted from particularly active phases of erosion in certain of them is suggested by the findings of the current study. Such a conclusion had already been reached by Johnson (1942) as a logical consequence of his multiple factor hypothesis conceiving the origin of the Carolina "bays."

Summary

Evidence based chiefly on the age and morphologic features of cypresses growing away from shore and on the degraded appearance of the peat along shore and in isolated "islands" surrounding some of these cypresses suggests strongly that the lake areas have been undergoing a modest phase of erosional expansion during at least the past 500 years. The author considers it likely that similar or even more extensive expansions, alternating with phases of filling and contraction, have occurred at various times in the ontogeny of these basins.

Such periods of erosion are important in the pollen and spore succession of the sediments in bringing about a mixing of microsfossils from earlier periods with those currently accumulating during such periods of erosion. Aggressive expansion of particular bays is also an alternate explanation for the interruption of the otherwise regular oval outline of one bay by that of another bay.

Succession in this hydrosere may well follow the pattern outlined by Buell (1939) of pioneer cypresses accumulating islands of shrubs around their bases, aided by a marginal encroachment of bay shrubs. The present author believes that accumulation of offshore sediments eventually permitting extensive interruptions of the previously continuous hydroperiod with only a moderate low-

ering of the water level, would be a more likely early stage in the succession than the direct advancement of cypresses into deep water.

The extensive filling of these lakes, which on the basis of the Singletary Lake pollen analyses (Frey 1951, 1953) has occurred largely since the broadleaf maximum in post-glacial time, has been more rapid at the northwest end than elsewhere. The present phase of erosion is involving the entire shoreline.

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REACTION OF SOILS: FACTS AND FALLACIES[1]

pH: Symbol and Reality

Scientists are not free from human weaknesses and are often taken in by fashionable innovations. This natural tendency has one unfavorable aspect: the period of infatuation with a vogue often gives rise to erroneous concepts which persist in textbooks and contaminate science with misleading generalizations.

The progress of physical chemistry, revealing the behavior of electrolytes, brought to the foreground the effect of free hydrogen ions. This soon became the prevailing fad of scientists dealing with soils and plants. Not so long ago, many agronomists and foresters were inclined to interpret all problems of soil fertility in terms of pH value and to ignore the effect of other factors. As information on the reaction of soils has increased, however, the central concept of the free hydrogen ion influence has become more and more distant from the circumference of actuality.

The symbol pH, introduced by Sørensen in 1909, was intended to express the concentration of hydrogen ions in aqueous solution ($-\log_{10}C_{H+}$). The values for the molar concentration (C_{H+}) were calculated from the equivalent conductivities, assuming that strong electrolytes are only partly dissociated in dilute solutions. The latter idea proved to be erroneous, and the Sørensen pH scale was found unsatisfactory (Moore 1950: 472).

The pH value is usually determined by potentiometric measurements of a cell's *emf*. Hence, it expresses the activity rather than the concentration of hydrogen ions. Therefore, we must accept today that pH is simply a number read on a potentiometer, preferably that employing a glass electrode.

Empirical as it may be, the pH value exerts a definite influence upon the life functions of organisms, availability of nutrients, and physical properties of soils. This value can serve as a useful tool in the management of soils for the production of farm and forest crops. However, the concept of pH must be freed from the misapprehensions which have been attached to it during the past thirty years. This should be particularly true in regard to generalizations such as those recently expressed by Pearsall (1952: 50) in whose opinion, "it may safely be said that the soil pH remains as the most useful single measurement that can be made for ecological purposes."

Effect of Hydrogen and Hydroxyl Ions on the Growth of Plants

According to earlier beliefs, hydrogen ions in the soil solution exert an injurious effect upon the root systems of crops. This idea apparently was brought into existence by observations of the effect of different acids in artificially prepared cultures. Today, the validity of this assumption appears to be definitely disproved by experiences in both farming and silviculture.

The work of Arnon and Johnson (1942) with tomatoes, lettuce, and Bermuda grass raised in nutrient solutions has shown that profoundly adverse effects of hydrogen and hydroxyl ions, *per se,* are revealed only at extremes of acidity or alkalinity, *i.e.,* at pH 3 and 9. As reported by Åslander (1952: 181), barley was found to grow equally well in nutrient solutions of common concentration at a range of pH 3.75 to pH 6.75. The same author presented results of experiments in which fertilized red clover, wheat, sugar beets, and other presumably acid-intolerant plants produced very high yields at low pH values. On the basis of his studies, Åslander arrived at the conclusion that the low productivity of acid soils is not caused by soil reaction, but by a deficiency of nutrients, and that no profitable increase in yields is achieved by liming of standard fertilized soils (p. 193).

In some instances, the ill effects of acid soils are due to the fixation of phosphates in the form of insoluble compounds. This process is especially pronounced in soils deficient in organic matter. As demonstrated by Gaarder and Grahl-Nielson (1935), the reaction between pH 2.0 and pH 8.0 is without influence on the solubility of phosphates in the presence of humus extracts. The addition of phosphate fertilizers together with manure was found to be an effective means of counteracting fixation of phosphorus in certain soils (Stephenson 1948).

Experience with forest tree seedlings provides many illustrations of the fact that the toxicity of hydrogen ions has been grossly exaggerated. Healthy pine and spruce seedlings are raised in hydroponics at a double or triple rate of normal growth at a reaction of pH 3.5 (Olson 1944), and in some cases even at a reaction approaching pH 3.0.

In order to control damping-off disease, nurserymen saturate the seed-bearing layer of soil with a 2 per cent solution of sulphuric acid (Wilde 1937), thereby raising the concentration of hydrogen ions in soil solution to nearly 0.01 g per liter. Yet, this drastic treatment does not preclude germination of the seed and normal development of the seedlings, provided they receive an adequate supply of nutrients from the lower untreated portion of the soil or from the applied liquid fertilizers.

Within certain limits, hydroxyl ions behave in a way similar to hydrogen ions. The low productivity of many alkaline soils is due to the deficiency of nutrients (Truog 1950), rather than an injurious effect of hydroxyl ions. Strong alkalinity of soil, exceeding pH 8.0, however, is associated with the presence of toxic compounds, *e.g.,* sodium carbonate, and is much more detrimental to plants than soil acidity.

One of the negative characteristics of alkaline soils is the abundant population of microorganisms which often handicap the normal development of plants. As has been shown by previous studies (Wilde 1946a), the harmful influence of lime applied to nursery soils is not because of the increased reaction or the presence of free carbonates, but because of the stimulated microbiological activity and consumption of available nitrogen.

In many instances, extreme pH values are correlated with unsatisfactory physical properties of the soil, particularly the occurrence of either hardpan or softpan layers. The latter condition is of special importance in silvicultural work, either in the selection of planting sites or in partial cuttings of forest stands.

The pH Value of Soils and the Distribution of Plants

The literature of today presents the optimum ranges of soil reaction for numerous cultivated and autochtho-

[1] Contribution from the Soils Department, Wisconsin Agricultural Experiment Station, Madison, Wisconsin.

nous plants (Spurway 1941). Such data give, at best, a very crude approximation of reality, and in many instances they are misleading.

Most of the reaction ranges were established by observing the distribution of plants in nature, a method which has little scientific justification. The occurrence of different species within certain ranges of soil reaction can be caused by numerous conditions other than the soil pH value, such as physical makeup of soil, content of available nutrients, presence of toxic substances, influences of climate, and competition of other vegetation.

The narrow natural reaction range of red pine between pH 5.0 and pH 6.0 is not imposed by the direct effect of either H^+ or OH^- ions; this range is delineated by two biological barriers—competition of white pine on strongly acid podzolic soils and destructive activity of damping-off fungi in circumneutral and alkaline soils.

The reaction of soils is not affected by the content of buffering substances, such as humus and clay. Therefore, reaction does not express the amount of H^+ or OH^- ions present, *i.e.*, the total acidity or total alkalinity of the soil. At times, the latter properties are of much greater ecological importance than the pH value. Siliceous sands, with a sprinkling of calcareous dust, as well as slightly weathered limestone outcrops, analyzing 70 per cent of $CaCO_3$ equivalent, have the same reaction of pH 8.0. Yet, sandy soils of this reaction may support healthy and rapidly growing plantations of Scotch pine and other lime-intolerant species, whereas highly calcareous soils induce chlorosis or root-rot even in pronounced basophilous hardwoods.

There are many indications that distribution of native vegetation is governed by the content of available nutrients to a greater degree than by soil reaction. In northern Wisconsin, strongly podzolized and extremely acid clays, underlain by fertile lacustrine substrata, support a highly diversified cover including many supposedly basophilous trees and ground cover plants. The lesser vegetation of these soils is characterized by an abundance of the introduced species of clover and other legumes. According to Åslander's observations in Sweden (1950), the distribution of Norway spruce, European birch, oak, basswood, and beech is influenced by the nutrient content of soil, particularly readily soluble phosphorus, far more than by the pH value of soils. Observations of Stone (1944), made on silty clay loams of Ohio, have shown that the distribution of American beech, hard maple, and several of their associates is independent of the pH value of the soil within the pH range investigated. Exacting American hardwoods, *e.g.*, white oak, tulip poplar, beech, and sycamore, show an exceptionally high rate of growth on heavy soils of Indiana and neighboring states at a reaction as low as pH 4.6 (Wilde 1950). The suggested optimum pH ranges for tulip poplar and sycamore are 6.0-7.0 and 6.0-7.5, respectively (Spurway 1941).

Conditions of climate appear to exert a particularly strong modifying influence on the range of soil reaction suitable to different plants. In the continental environment of the Lake States, black spruce is confined to strongly acid soils; in highly humid regions of Canada, the same species thrives on calcareous deposits and circumneutral peat soils underlain by alkaline ground water (Pierce 1953). Hemlock and balsam fir are at the top of the list of acid-preferring or acid-tolerant species. Nevertheless, in the humid belt bordering Lake Michigan, these trees grow successfully on calcareous soils of pH 7.3 to pH 8.0. Hence, once again we must acknowledge the correctness of the old paradox of Pfeil (1860): "In forestry there is but one general rule: namely, that there are no general rules."

What is said about trees is equally true of lesser vegetation. Under suitable climatic conditions, the most pronounced acidophilous plants like *Rumex acetosella, Ledum groenlandicum,* and *Chamaedaphne calyculata* thrive on soils of alkaline reaction, even on outcrops of limestone. *Ledum groenlandicum* in a humid climate attains particularly luxuriant development on calcareous substrata; its suggested optimum reaction range is between pH 3.0 to pH 5.0 (Spurway 1941).

These observations should suffice to illustrate the fact that the relationship between the pH value of soils and the distribution of plants is complicated by the influence of many other factors and hence does not permit broad generalizations. Such generalizations are particularly unsound when investigations are made with no regard to the climatic-zonal pattern of the world—a pattern embodying soils of different genesis with their corresponding types of vegetative cover and groups of soil organisms.

Role of pH Value in Soil Development

Prior to systematic studies of North American soils, the expression "blackearth" was synonymous with the Russian "chernozem," a humus-enriched soil characterized by a neutral or alkaline reaction and by the presence of a horizon with accumulated calcium compounds. The high pH value of chernozems and a high concentration of soluble salts were considered among the conditions precluding forest growth and instrumental in the development of grassland soils. Investigations by American soil scientists (Marbut 1935), however, revealed the existence of an enormous area of chernozem-like "prairie soils" that possessed an acid reaction, a low concentration of soluble salts, and no zone of calcium carbonate accumulation. This discovery clearly demonstrated for the first time, the great pedogenetic potential of biological factors and the subordinate importance of pH value in the development of grassland soils.

The commonly accepted explanation of the genesis of podzol soils (Glinka 1908, Gedroiz 1929) implies the action of organic acids which are formed as by-products of the incomplete decomposition of organic remains. The acids first remove the bases and then presumably cause the reduction and translocation of iron and aluminum sesquioxides. These ideas of the purely chemical nature of the podzolization process persisted in the literature for a number of decades. Recently, however, they have met with sharp criticisms from the geochemist Vernadskii and his followers who stressed the importance of microbiological factors in the processes of soil development and pointed out several factual errors in the assumptions of pedologists. The errors were particularly concerned with the effect of hydrogen ions on the behavior of colloids and the translocation of aluminum sesquioxides (Vernadskii 1939, Geltzer 1950).

The reports on the wide occurrence in Canada of strongly podzolized "grey wooded" soils possessing circumneutral reaction (Williams and Bowser 1952) took the argument outside the realm of theoretical speculation and proved conclusively that hydrogen ion concentration is not a causal factor in the processes of podzolization. Similar observations were also reported from another part of the British Empire—Australia, by Costin, *et al.* (1952). These investigators state: "The processes of podzolization are not necessarily related to soil acidity, since the most podzolized soils occur in the montane tract under the least acid conditions and the unpodzolized

soils in the sub-alpine and alpine tracts under conditions of stronger acidity" (p. 207).

It is interesting to note that "calcareous podzols," formed on dolomitic deposits and essentially similar to Canadian "grey wooded soils," were described 40 years ago by the Russian forester Tkachenko (1911) in his report on soils of Archangel province. If Glinka and other pedologists had paid attention to this report, the theory of soil genesis might have been spared at least one serious misapprehension.

Unqualified generalizations also embrace the counterpart of the podzol—the non-podzolic soils whose profiles do not exhibit leached (A_2) and accumulative (B) horizons. Such soils are known under the name of "weakly podzolized soils,' "brownearth," "brown forest soils," "mull soils," and "melanized soils." They are formed in environments favorable to the activity of certain soil organisms which preclude the accumulation of raw humus. Non-podzolic soils, therefore, develop but one pedogenetic horizon, a mull layer with incorporated humus, which at times is covered by a veil of last year's litter.

The idea that nearly neutral reaction is essential for a rapid decomposition of forest litter and the stability of sesquioxides was probably inherited from the foresters' myth of "sour" origin of raw humus and "sweet" nature of mull humus. Investigations during the last two decades in both Europe and America have shown conclusively that the reaction of mull humus layers and soils with undifferentiated profiles varies within a wide range of about pH 4.5 and pH 8.0 (Hesselman 1926, Němec 1928, Romell and Heiberg 1931, Romell 1935, Frei 1946, Wilde 1946b, 1950, Lafond 1951, Duchaufour, Michaud, and Millot 1952, Mader 1953). The nearly neutral reaction of brownearth (pH 6.5 to pH 7.0), often stressed in European textbooks, is the result of the peculiar origin of this soil group which is confined to substrata rich in bases, such as limestone and ferro-magnesian rocks (Stebutt 1930).

Thus, a survey of recent literature on genesis of soils in the temperate region indicates that pH value of soil and corresponding chemical processes are not the primary causal factors of soil development. Whatever influence soil reaction exerts on the processes of soil formation, as a contributing factor, such influence is radically modified by climatic conditions. The changes induced by climate appear to affect particularly the type of soil microorganisms and their rate of activity. Present discrepancies in the theory of soil genesis should be in a great measure attributed to the failure of pedologists to consider biological factors as an inseparable part of the climatic-zonal pattern of soil development.

Summary

This critical essay is based on a survey of recent reports and the personal observations of the author. It acknowledges the important influence of reaction on the activity of soil organisms, availability of certain nutrients, and structure of soils. It points out misconceptions which exist in literature in regard to the direct effect of reaction on the growth of plants, distribution of vegetation, and development of soils.

The author supports Åslander's contention that, in the presence of a sufficient supply of available nutrients, the concentration of hydrogen ions found in soils is of minor importance to the growth of plants. This is substantiated by the fact that basophilous plants are raised satisfactorily in fertilized soils or nutrient solutions at critical reactions below pH 4.0. Within certain limits, the low productivity of alkaline soils is caused by the unavailability of certain nutrients, consumption of available nitrogen by microorganisms, or destructive activity of parasites, and not by the concentration of hydroxyl ions. Strong alkalinity, however, is correlated with the presence of toxic compounds and is much more detrimental to plants than soil acidity. The unfavorable effects of extreme pH values are most pronounced in soils deficient in organic matter.

The validity of suggested reaction optima for different species, established by observation of natural plant distribution, is questioned. Occurrence of a species within a certain range of soil reaction is often caused by factors other than the pH value, *e.g.,* physical makeup of soils, climatic influences, competition of other vegetation, and effect of parasitic organisms. Examples are given of pronounced acidophilous plants (hemlock, balsam fir, black spruce, sheep sorrel, and Labrador tea) and basophilous plants (tulip poplar, sycamore, clover and other legumes) which in suitable environments grow well on alkaline (pH 7.3-8.0) and strongly acid (pH 4.6) soils, respectively. The ecological importance of the total acidity and total alkalinity is stressed.

The wide occurrence of acid prairie soils, calcareous podzols, and extremely acid non-podzolic mull soils is quoted as a proof of the secondary importance of soil reaction and correlative chemical transformations in the processes of soil development. In the opinion of the author, descrepancies existing in the theory of soil genesis are largely due to the failure of pedologists to consider biological factors as an inseparable part of the climatic-zonal pattern of soil development.

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PARALLELISMS BETWEEN ECOLOGY AND TAXONOMY

Although the present article is in agreement with Davidson (1952) in regard to the use of taxonomy in ecology, there would appear to be the need for a companion discussion of the converse situation, the use of ecology in taxonomy. While very carefully delimiting the aim of taxonomy as that of establishing relationship between individuals and expressing this through classification, Davidson has presented little more than a sketch of the aim of ecology. This failure to consider the aims of ecology in greater detail, however, could not be implied to invalidate his remarks, but it points to the fact that these aims may not be clear to many who deal with taxonomy. Also, it would be impossible to find agreement on such aims even among those more directly concerned with ecology, as is evident in the criticisms of American plant ecology as presented by Egler (1951). There is no intention of becoming involved here in a delimitation of the boundaries of plant sociology, plant ecology, plant distribution, and plant geography, if indeed such boundaries exist. For the purposes of this article the fundamental aim of ecological work may be considered as that of the understanding of the interaction of the individual and its environment. Then just as a taxonomist may be concerned with the sorting of a pile of specimens representing a very heterogeneous group of individuals into some sort of classification denoting the relationship of the individuals, the ecologist is concerned with the study of a heterogeneous group of individuals comprising the vegetation in his attempt to discover and to interpret their interaction with the environment. Although, in taxonomy, the relationship between two individuals may be rather precisely described, the relationships of increasing numbers of individuals become progressively more difficult to describe owing to the presence of fewer common characteristics. Likewise, in ecology, the interaction of one individual with its environment conceivably might be precisely determined. However, owing to variation between individuals the description of interactions of greater numbers of individuals with their environment becomes correspondingly less accurate.

Because they are essentially interpretive, taxonomy and ecology are basically synthetic sciences. Therefore, it would be as impossible to do fundamental research in "experimental" taxonomy, as in the same sense, it would be impossible to conduct a project in "experimental" ecology. For wherever we invoke the term "experimental" in regard to these two synthetic sciences, we are immediately and directly concerning ourselves with the experimental disciplines of physiology, morphogenesis,

or genetics. An "experimental" taxonomic problem of establishing relationships between two individuals, as Mason (1950) has pointed out is one of comparative morphology, comparative physiology, or hybridization. A project in "experimental" ecology intended to establish the interaction of the individual and its environment becomes a problem in morphogenesis and physiology. Furthermore, a study of the interactions of a species or other taxon with the environment or with varied environments is a problem in systematic morphology, systematic physiology, or systematic genetics.

From the foregoing, it would appear that the fields of taxonomy and ecology are syntheses of data from the same sources and hence must overlap. Therefore, for a realistic consideration of the basic problem of the interaction of an individual and its environment as involved in the question, "Why do plants grow where they do?", the ecologist must be concerned with the same basic disciplines which the taxonomist must use in attempts to understand the question, "What is the relationship existing between these plants?". Both the taxonomist and the ecologist may profit from the work of Kerner (1895), Turesson (1922), and Clausen, Keck and Hiesey (1940, 1948). These men have made clear the essential nature of the species, an important part of which is the recognition of physiological variability between individuals. The nature of the species, as defined by these workers, means to the ecologist that he must be aware of genetic differences from one individual to another within the same species, and means to the taxonomist that he must be aware of the interaction of the individual with the environment if a full understanding of the significance of infraspecific variation is to be attained. Seemingly, investigations on the nature of the species are basic to both taxonomy and ecology and as such become the "property" of both sciences. As is evident in the recent article by Constance (1953), much of the research which has gone under the guise of biosystematics has involved both a taxonomic and an ecologic viewpoint and as such has yielded significant contributions to both taxonomy and ecology.

In conducting a taxonomic study, the taxonomist must acquire an adequate sample of the taxon under investigation. In this sampling process, number alone should not be the primary consideration, but presumably the taxonomist must acquire an adequate sample from the environmental niches in which the taxon is present, if the sampling is to represent a full range of morphological and physiological expression. In altogether too many examples, sampling techniques are carried on with little or no awareness of variation over the habitats concerned. It would appear that sampling techniques in many cases are conducted in order to supply dots over a distributional map and as such may fail to give proper orientation as to the different environmental situations which may be involved. In preparing a monograph of a widespread genus, faulty sampling technique might inadvertently lead to a misconception of relationships. The same faulty technique could produce a taxonomic evaluation which failed to include the full range of morphological expression even in a narrowly restricted monotypic genus. Likewise, sampling techniques in ecology which are conducted without a consideration of the variation between individuals from one area when compared with those representing the same species from another area are apt to lead to erroneous conclusions in regard to the vegetation. It would appear necessary in effective sampling that the taxonomist consider the point of view of the ecologist, and, conversely, that the ecologist consider the point of view of the taxonomist if an "adequate sample" is to be acquired in either taxonomy or ecology.

A taxonomist dealing with a generic revision, no matter how diligently he pursues his field work, is perhaps incapable of covering the entire distribution of the taxon except in the case of a very narrowly restricted one. Therefore, out of necessity, he must resort to the material available to him in the herbarium. While plant collectors have largely remedied the fault of inexact locations, seldom representing them by one word, such as "Iowa" or "California," as was once common practice, they have as yet paid little attention to the exact environmental conditions in which the specimen was found. We are still plagued by data accompanying herbarium material which is no more precise than "Prairie" or "Roadsides." One might effectively counter these remarks, however, by asking: "What ecologist knows what is taxonomically significant?" and "What taxonomist knows what is ecologically significant?". At this stage in our science, we can only plead for more complete data without suggesting what may be significant. It might be possible to suggest an ideal for plant collectors in regard to inclusiveness from the standpoint of both taxonomy and ecology. However, we should be realistic in what we can expect to find in the herbarium, and be aware of the meagerness of much of the material and accompanying data which has been collected.

For a taxonomist to state the relationship of plants which he has not seen growing in nature would appear to place these conclusions in a precarious position. Likewise, for an ecologist to make positive predictions of the pH or base exchange capacity of the soil from looking at a photograph of the vegetation of an area which he has never investigated would appear to place these predictions in an equally precarious situation. Yet, with regularity and rapidity, certain taxonomists are complicating nomenclature and classification by the assignment of names to unicates with which they have had no closer contact that that permitted by a lens. Such a criticism cannot be made without the inclusion of the parallel consideration of ecological workers who do little more than photograph an area and then subsequently increase the complexity of ecological nomenclature without knowing the plants with which they are dealing or knowing the interaction of any individual and its environment. Furthermore, the possibility exists for an ecologist to hire someone to study taxonomic nomenclature and to identify the plants with which he is working. In fact, ecologists regularly report that the identification of plants used in their study was performed by another person. Moreover, this would appear to be removed only slightly from the parallel situation of the taxonomist hiring a person to study the nomenclature of vegetational units and from this to identify the environmental conditions in which his plants are growing. Regularly, information in taxonomic monographs is being based upon environmental data which is provided by plant collectors who have ventured into the field with little or no means for recording any precise information.

While the opinions in the foregoing paragraph would appear to display little understanding of the difficulties with which the taxonomist and ecologist must deal in their efforts to solve problems, it is suggested that the attempt here is not one of judging the work of others but is one of simply stating the parallel problems with which ecologists and taxonomists must cope. It is equally possible for an ecologist to criticize taxonomic work and for a taxonomist to criticize ecological work. The point which should be raised, however, is whether a

position of mutual understanding might not be more advantageous for both scientists.

Since neither ecology nor taxonomy can progress beyond the extent to which documented facts are provided by studies in the basic disciplines of morphology, physiology, and genetics, it would appear that weaknesses of taxonomy, therefore, would also be weaknesses of ecology and likewise, that weaknesses of ecology would be weaknesses of taxonomy. Both taxonomists and ecologists are concerning themselves with the same basic data, and seemingly each could draw faulty conclusions if there were a failure to consider the point of view of the other. Some harmonious pattern for research involving the aims of taxonomy and the aims of ecology would appear to be an attainable goal for both fields in order to present valid conclusions in each of these phases of science.

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SURVIVAL OF PLANTS UNDER FLOOD IN THE LOWER FRASER RIVER VALLEY, BRITISH COLUMBIA

The highest flood levels, experienced on the Fraser, Nooksack, Skagit, Columbia, and other river systems of the Pacific Northwest for over half a century, were reached during June and July, 1948. Rapidly growing vegetation on large acreages of cultivated land, bush, and forest were inundated; most of the acreage had not been flooded for decades and some perhaps not for a century. With considerable interest, the author recorded the striking differential killing by flood waters, of species of higher plants, especially on the lower reaches of the Fraser and Columbia rivers.

Only a very general assessment of the effects of the flood waters on different species could be made. Quantitative studies of the vegetation, made prior to flooding, were lacking. It was observed that lethality of the waters was associated with their temperature, depth, duration, and movement. These variables and their influence on the higher plants could, quite probably, in turn be related to the relative concentrations of dissolved gases in the water. Certainly cold, swift water did little but delay the growth of most species and cause a certain amount of mechanical injury; slow moving or stagnant, warm water, on the other hand, caused the death of nearly all aerial vegetation after a day or two under flood. In spite of the complex interactions of the flood variables, some comparative observations seem to be worth recording.

A number of peat bogs were inundated and fine silt was deposited in a thin layer over them. The principal species of the bogs, Labrador tea (*Ledum groenlandicum*), blueberries (*Vaccinium uliginosum*), bog laurel (*Kalmia polifolia*), hardhack (*Spiraea douglasii*) and *Sphagnum* spp., though silt-covered, suffered no obvious injury. In one bog near Walnut Grove, B. C., young western hemlock (*Tsuga heterophylla*), (about 50 trees per acre), which had become established in the bog or on its periphery within the last few decades, were killed. Spruce (*Picea sitchensis*), growing in the same areas and developing in recent decades, suffered considerably, as evidenced in yellowing, die-back, and needle-drop, but were rarely killed. Lodgepole pine (*Pinus contorta*), the principal tree species about the bogs, also showed some chlorosis and die-back.

Over ox-bow meadows and marshes, the flood waters, perhaps because of their stagnation, were often very lethal. On such areas, above-ground parts of nearly all sedges (*e.g., Carex rostrata*) died, but soon after the recession of the flood, new growth came from rhizomes. By October of the flood year, many of the sedges had matured a fair crop of seed. Strikingly, reed canary grass (*Phalaris arundinacea*) and mannagrass (*Glyceria* spp.) survived bright and green in the midst of dead sedge. *Juncus effusus*, a coarse bunchy rush and a common weed of wet pastures, known to survive weeks of flooding in winter, was extensively killed. Hardhack (*Spiraea douglasii*), a common rosaceous shrub of the meadow margins, frequently suffered defoliation but small leaves soon came to replace the old on the gaunt shoots. Old willow trees (*Salix hookeriana*) were killed where young trees survived. As the waters rose on the trunks of cascara (*Rhamnus purshiana*) and hazel (*Corylus rostrata*) their foliage developed brilliant colors. Some of these trees died in the course of the year.

Much of the flooded lowland remaining in forest is given over to a sub-climax, mixed conifer-hardwood community. Of the conifers, Douglas fir (*Pseudotsuga taxifolia*) succumbed most readily to flooding at base; western hemlock (*Tsuga heterophylla*) also suffered markedly. Red cedar (*Thuja plicata*) developed a brilliant orange chlorosis but seemingly suffered no further injury. Spruce (*Picea sitchensis*) rarely suffered. Among hardwoods, the native wild cherries (*Prunus emarginata*) rarely survived even a "low" flood of a few days' duration; over the area flooded scarcely a tree of this species can be found today where formerly they were quite common. Wild apple (*Pyrus rivularis*), on the other

hand, showed little or no injury. Elder (*Sambucus callicarpa*) often died but regenerated readily from the crowns. Dogwoods (*Cornus stolonifera* and *C. nuttallii*) and black cottonwood (*Populus trichocarpa*) suffered little more than occasional chlorosis. Some broad leaved maple trees (*Acer macrophyllum*) succumbed, particularly if they were growing very actively. Red alder (*Alnus rubra*) died in large numbers and was regarded as one of the most susceptible of all trees to damage by flooding; Sitka alder (*Alnus sinuata*) was not affected to the same degree.

Flood waters killed the top growth on large acreages of pasture and cropland. Bunchgrasses such as timothy (*Phleum pratense*), orchard grass (*Dactylis glomerata*) and perennial ryegrass (*Lolium perenne*) died readily. Sod grasses, Kentucky bluegrass (*Poa pratensis*), bentgrass (especially *Agrostis stolonifera*) and quack grass (*Agropyron repens*) soon revegetated, from underground parts, many areas where they existed before the flood. Horsetail (*Equisetum arvense*) and sheep sorrel (*Rumex acetosella*) too, developed rapidly from rhizomes. Clovers, even Alsike clover, quite generally died. However, white clover (*Trifolium repens*) frequently regenerated from stolons, and seeds of red clover germinated in unexpected numbers in the mud left by the retreating flood. Annual weed seeds of species too numerous to name germinated freely on the mud and sand of former hay and pasture areas. Spring seeded grains did not withstand even light flooding.

Our records of the effects of the flood on cultivated species, other than grasses and legumes, are numerous but are so scattered that comparisons are difficult to make. The following are a few of the apparently more reliable observations. Very susceptible to death and damage by the flood waters were holly (*Ilex aquifolium*), filbert (*Corylus avelana*), raspberry var. Cuthbert, lilac (*Syringa vulgaris*), mock orange (*Philadelphus gordonianus*), cotoneaster (*Cotoneaster* spp.), cherry, rowan tree (*Sorbus aucuparia*), cherry laurel (*Prunus laurocerasus*), cryptomeria and certain unidentified junipers. Less susceptible, but often killed or severely damaged, were many trees (*Crataegus oxyacantha*), box (*Buxus sempervirens*), and Himalayan blackberry (*Rubus procerus*). Some damage, as shown by chlorotic leaves and so forth, was suffered by the evergreen blackberry (*Rubus laciniatus*), pears, roses, grapes, rhododendrons, and black locust (*Robinia pseudoacacia*); generally without evident damage were apples, walnuts, Manitoba maple (*Acer negundo*), and chestnuts.

Some of the observations from the Pacific Northwest floods of 1948 are confirmed by observations made elsewhere or in other circumstances. Lawrence (1939) noted the intolerance of the Douglas fir to flooding in the gorge of the Columbia River. Klose (1927), too, noted the susceptibility to damage of this species, of *Prunus avium*, and of certain *Alnus* spp., and the tolerance of *Pinus banksiana* (a congener of *P. contorta* mentioned above), and *Populus* spp. Anderson (1927) noted the marked susceptibilty of *Prunus avium* and *Sorbus aucuparia*. Parallel observations respecting forage grasses and legumes, and weeds are likewise found in the statements of McKenzie, *et al.* (1949) and Savile (1951) and many others.

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A NOTE ON THE STABLE POINT OF POPULATIONS SHOWING BOTH INTRASPECIFIC COOPERATION AND DISOPERATION[1]

A humpback curve frequently results when some representative measure of the well-being of a population is graphed as a function of population density (Allee 1940, 1951: 31, Allee *et al.*, 1949: 396). Such curves make use of many types of measures of the condition of the population for a great variety of organisms. It can be said, therefore, that the humpback curve is sufficiently frequent to be a generalization.

In the present discussion, the specific survival rate, which is the specific birth rate minus the specific death rate, is used as the measure of the immediate condition of the population. Ludwig and Boost (1939) plotted this population parameter as a function of density; they used data from several authors and thus demonstrated such humpback curves as are shown in Figure 1. This constitutes confirmation of the generalization in terms of survival rates and a demonstration that the simple logistic equation does not apply in these cases. A logistic has a slanting straight line in this plot. The humpback curve indicates that the distribution of beneficial and detrimental density dependent factors affecting the excess of births over deaths generally produces a maximum survival tendency at a moderate population density. Those populations that lack the humpback and left slope of the curve (Figure 3A) can be considered to be special cases of the general curve which have the optimal survival tendency at the lowest possible density.

Customarily, the left portion of the curve is referred to as a zone of cooperation. Until the density is above the optimum, there is an increase in survival tendency as the density increases. The right side of the curve to the right of the hump is referred to as the zone of disoperation, since the survival tendency decreases as the density increases.

A hump-shaped curve like the one in Figure 2 can be

[1] We are grateful for suggestion and comment by E. S. Deevey, P. W. Frank, E. P. Odum, T. Park, and P. G. Pearson.

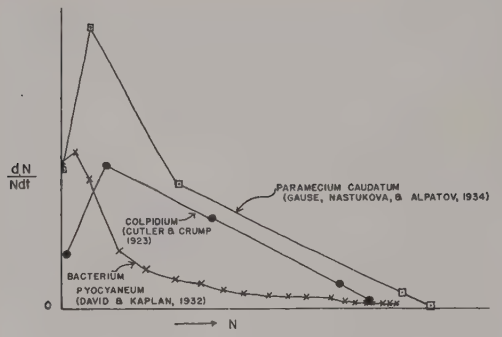

FIG. 1. Specific rate of population change as a function of density (modified from Ludwig and Boost 1939). Coordinates are adjusted to permit comparison of curves.

expressed in the form of an equation for clarity as is shown below. This expression avoids the difficulty of introducing a fictituous biotic potential or requiring determination of the intrinsic rate of natural increase which is determined with difficulty. Instead b represents any operationally determined growth rate.

This discussion strictly applies where there is only one specific growth rate for each density. If the organism changes its basic nature, or if the environment is not kept constant, the curve will change. Therefore, the density growth-rate curve should be used for comparisons in open steady state systems. Some of the curves from Ludwig and Boost (1939, Fig. 16) do not properly meet this requirement in the higher density range where waste product accumulation causes change in the growth rate even at identical population densities.

$$\frac{dN}{N\,dt} = b + f_1(N) - f_2(N)$$

N Is the population density

t Is the time

$\frac{dN}{N\,dt}$ Is the specific survival rate (specific growth rate)

b for operational simplicity, is the specific growth rate of some small population under favorable and reproducible environmental conditions. (The assumption of an intrinsic rate of natural increase with a stable age distribution does not seem necessary to the study of the density-dependent factors.)

$f_1(N)$ is some positive function of N representing intraspecific cooperation effects. This term contributes component curve B in Figure 3.

$f_2(N)$ is some negative function of N representing disoperative effects.

When the cooperative term is zero, the remainder of the equation contributes component curve A in Figure 3. The basic biotic potential term b, the cooperative term, and the intraspecific disoperative term together produce the humpback curve that relates the specific survival rate to the population density. Note how the overall curve becomes concave on its right leg as a result of cooperation as suggested by Ludwig and Boost (1939).

The stability principle discussed by Holmes 1948 suggests that systems trend toward a stationary steady state by the natural selective elimination of all states that are not stable. A stable state is here defined as one with a self-regulating mechanism so that if the system is displaced from its stable state it will return like a cork bobbing on water. Biological natural selection has been considered a special case of the stability principle (Holmes 1948), and applications have been suggested for geochemical systems (Odum 1951).

The stability principle suggests that regardless of its initial state, a population of organisms will either increase or decrease until a population density is reached that is characterized by a self-regulating mechanism. A point on a graph with a self-regulating mechanism can be referred to as a stable point as has already been described in inter-specific competition systems by Gause (1935). As indicated in Figure 2, there is only one stable point for a population that possesses a survival-density curve of the types in Figure 2 or Figure 3A. The stable point is the intersection of the curve with the zero line of equal births and deaths on the right side of the hump. Here, stability results from a self-regulating mechanism. Should the population increase, deaths would begin to exceed births and the population would decrease to the stable point again. Should the population decrease past the stable point, births would exceed deaths and again the population would return to the stable point. A population whose density is in the zone of disoperation will move to the stable point.

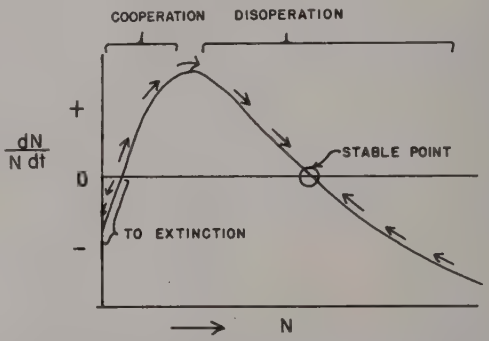

FIG. 2. Generalized survival-density curve characteristic of populations which have a negative survival rate at low densities.

On the left side of the hump, the population behaves in a different manner. Should the population possess a density in the cooperative range above the line of equal births and deaths, the population will move to the right and eventually end up at the stable point on the right side of the hump. Should the population possess a density below the birth-death balance line on the left, unless conditions change it would move to extinction. Thus, no population can remain at a density in the cooperative zone for there is no stable point there. Isolated populations cannot, therefore, conceivably survive without some form of disoperative intraspecific competition in operation. They will either become extinct or increase until a disoperative intraspecific competition does begin to operate. Applying this conclusion to human populations, one might state that non-competitive utopias are unstable and impossible unless, of course, some new kind of self-regu-

lating mechanism can be introduced to permit a stable point on the left side of the hump.

The absence of a stable point on the left side of the curve helps to explain why cooperation among organisms is often overlooked. The important question arises: why is cooperation so widely distributed in the living kingdoms even though populations are rarely found in the density range corresponding to predominantly cooperative interaction? It is suggested that the presence of cooperation in a species has the function of raising the density of the stable point thus giving a species an edge in competition with other species. In terms of the equation above, the cooperative term illustrated in Figure 3B when added to the remainder of the equation in Figure 3A produces a curve in Figure 2 whose stable point is shifted to the right. Thus, other things being equal, cooperative animals have higher densities in their stable population levels than non-cooperative animals. But in all cases, the stable point is characterized by an excess of disoperative competition over cooperation. The intraspecific cooperative effect above may be either linear or a more complex function such as the second power term suggested by Hutchinson (1947) for social animals.

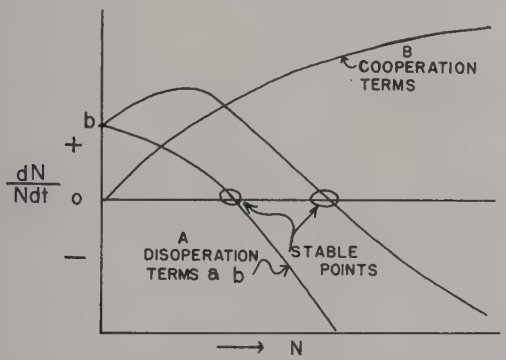

FIG. 3. Survival curve and components for a species with a survival rate that is positive at minimum densities.

In man's evolution, we have apparently had continual shifting of the stable point to the right as man's cooperation increased. The great question before us all is not how to increase cooperation or how to avoid the inevitable disoperation but what form of disoperation will ultimately determine our stable point and at what density will this take place.

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AN EARLY VIEW OF THE RELATION BETWEEN PLANT DISTRIBUTION AND ENVIRONMENTAL FACTORS

A feature of ecology in recent years has been the drift away from mono-climax concepts of vegetation and toward a factorial approach, which emphasizes that plant distribution is conditioned by interactions between several environmental factors capable of independent variation (Cain 1947, Major 1951, Billings 1952). Modern ecologists may, therefore, be interested to learn of a parallel situation existing in Britain over a century ago.

During the early part of the nineteenth century a number of articles were published ascribing differences in plant distribution mainly to single factors, such as differences in rocks or climate. In an attempt to reconcile the various opinions on this matter, H. C. Watson published in 1833 a paper entitled "Observations on the Affinities between Plants and subjacent Rocks," where he stated: —"It is . . . necessary that all conditions of vegetation distribution be studied in connection. He who neglects any, will so far fail in his generalizations." After a brief illustration of this point of view, he proceeded to a series of conclusions concerning the factors controlling plant distribution. Since these anticipate present-day principles of plant geography and ecology, it may be worthwhile to quote them in full, as follows:—

"I. The principal conditions of vegetable distribution should be arranged in the following order; the first-named being of greater sway than those which succeed, and consequently a small difference in the former operating more change than a great dissimilarity in the latter:—1. Temperature; 2. Moisture; 3. Configuration of surface (chiefly with relation to shelter and exposure); 4. The mechanical and chemical properties of the surface soil; 5. The mechanical and chemical properties of the subjacent rocks.

"II. The *combined influence* of these, with some minor conditions, determines the flora and vegetation of countries.

"III. As to comparative influence, these conditions are not always in equal ratio or proportion; but, when the

more potent condition or affinity is in its full play, the feebler one is less apparent; and *vice versa*. Thus, when the temperature is best suited to any given species, soil is of little moment; but when the temperature barely suffices, then soil may determine even the existence of the species.

"IV. Comparing these conditions with each other, the influence of temperature (being less local) is chiefly shown in the flora of a country; while other conditions (often partial in their sway) may not at all affect the flora of a considerable tract, and yet greatly modify its vegetation; the latter term having reference to the comparative prevalence, the former to the mere existence, of the *species*.

"V. Comparing one species with another, some are more influenced by one, some by another of the above conditions. Some, for example, have a wide range of temperature, others are indifferent to soil or moisture.

"VI. With regard to subjacent rocks, their influence is so frequently veiled by the other conditions, that for the most part the flora of a country is not obviously affected thereby, though the vegetation of small tracts may evidently betray it."

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THE OCCURRENCE OF A MAYFLY NYMPH IN BRACKISH WATER

Circumstantial evidence has been available for some time indicating that the nymphs of *Callibaetis floridanus* Banks may inhabit brackish water (Berner 1950); however, no salinity determinations were made to substantiate this evidence. In 1949, the senior investigator collected nymphs of this species of mayfly from around the roots of the red mangrove, *Rhizophora mangle* L., south of Homestead, Florida. Because of the flooded conditions in the Florida Everglades, the water around the tree at that time was definitely fresh.

The junior investigator, while studying the insect fauna of Homosassa Springs, which empties into the Gulf of Mexico north of Tampa, Florida, found that the nymphs of this species were present in water which appeared to be definitely brackish. Further investigation and analysis of the water proved that the insect can tolerate rather high salinities.

The collecting stations from which the nymphs came are approximately one mile inland from the Gulf and are subject to tidal fluctuations. At low tide, chloride values in parts per thousand at the collecting sites were 2.13 (3.92 total salinity) and at three hours past high tide 4.43 (8.15 total salinity). It is estimated that at the peak of high tide the salinity must be somewhere near 10 parts per thousand. Dissolved oxygen ranged from a minimum of 4.62 to a high of 7.02 parts per million.

The nymphs were found on the leaves of the aquatic plants *Potomogeton pectinatus* L. and *Vallisneria neotropicalis* M.-V. No other mayfly species were encountered although nymphs of the damselflies *Ischnura ramburii* (Selys), *Enallagma durum* (Hagen) and *E. pollutum* (Hagen), larvae of Tendipedidae and Heleidae, and the water striders *Trochopus plumbeus* (Uhler), *Mesovelia mulsanti* White, *Trepobates floridensis* Drake and Harris, and *Rheumatobates tenuipes* Meinert were found associated with the mayfly nymphs.

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[1] The studies of the junior investigator were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Florida (NR 163-106).

Agar's Individual Organism[1]

Man shares in common with most animals an extraordinary restlessness and activity, an activity which when we are not ourselves a part of it, seems like a rather meaningless expenditure of energy. Among men, the forms of this expenditure are manifold. Whether it is a child on a playground slide or an adult on a roller coaster, whether it is a builder of colossal power dams or an exploder of hydrogen bombs, whether it is the founder of a one-prophet esoteric cult or merely a selfless seeker after wisdom, the *philosophos,* there is a fundamental unity in the insatiable urge for activity. Some philosophers would have us believe that he who has a mind must perforce exercise it in an eternal quest to understand the world around us (A gentle gibe for those who are not philosophers and who, by the rules of the game, can have no opinion on the matter). That quest to understand the world of which we are a part can take many guises, from impersonal description and measurement, to lofty flights of thought that aim to break through the barriers of our mind, its senses, its dimensions, and its psychological urges. It is to this last category of flight that Professor Agar's volume belongs: it is an able penetrating analysis in a subject that few have dared to enter. Unhesitatingly he discusses and utilizes the findings of others, sometimes with a very commendable diffidence. Adding to these tools, he has explored, prodded, advanced, retracted. The reader is never made to think that the author is uttering a pseudo-divine revelation, which he must accept, or be cast among the eternally damned. Rather, here is an intellectual exercise, a sortie into outer space from the comparative stability of scientific measurements and experiments. There is a take-it-or-leave-it attitude that will appeal to those who wish to sail their own space ships, but not to those who want the simple satisfaction of being a paid passenger on some master ship they have chosen for its superficial glitter.

W. E. Agar, F.R.S., late Professor of Zoology at the University of Melbourne, was scientifically active in several branches of the science, mainly in studies of the invertebrates. Building upon a thorough grounding in physiology and psychology, and adopting Whitehead's philosophy of organism, itself stemming from mathematics and physics, his interests early expanded along philosophical lines. In 1944 the first edition of this book was published in Australia. Geography and war combined to limit the distribution of this volume, and in 1952 a new edition was prepared, published jointly with the Cambridge University Press.

It should be understood at the start that "organism" in Professor Agar's sense is an individual animal. Only indirectly does the term include the concept of species; most plants are excluded as not having the attributes he discusses; and all "super-," "quasi-", and "complex" organisms are outside the scope of the volume.

It is perhaps rashness if not folly for this reviewer to attempt to state succinctly the main thesis of the volume, and yet such a statement would have a distinct value to one approaching the book for the first time. It appears that Professor Agar's contention—and I doubt if he would consider it original with himself—is that available scientific knowledge seems to indicate that the organism acts both as a single "whole," and as composed of lesser wholes of various categories both in time and space; that fundamental behavior of all these subjects involves perception (feeling and experiencing) and purposiveness; and that thus causation and teleology are legitimate philosophic concepts in comprehending the organism (though not at all in the sense that ecologists usually speak of "cause," and laymen speak of "purpose").

Chapter I is "Introductory," and covers four distinct ideas, elaborated and justified in succeeding sections. The remaining five chapters are logically divided into what would appear to be consideration of three of the basic "points of view" towards a "subject matter," as used by the reviewer and other authors. Chapter II involves spatial considerations; III and IV treat of functional activities; and IV and V concern temporal phenomena.

In Chapter II, "The Unity of the Organism," the author, accepting the philosophy of holism, discusses various levels and categories of "central agents" and "sub-agents" that are spatially organized within and among its various parts. The concepts of biological field and brain field are included, as well as a summary of Gestalt psychology, and of our knowledge on cortical localization.

Chapter III, "The Organism as a Psychophysical System," is a consideration of that activity to which we generally refer with such words as "consciousness" and "purpose," when a mind-body relationship is involved. In order to remove justifiable opposition to the term "purpose" (as in the phrase, the purpose of the sexual instinct is the continuance of the species), the author adopts the twin concepts of "hormic goals" and "biological consequences." For example, mating is a hormic goal of sexual activity; the continuance of the species is merely the biological consequence of that mating. He chides us for calling the wasp stupid in its instincts, for completing nesting details when the eggs have been removed, and for acting to satisfy hormic goals alone. With his tongue in his cheek he reminds us that "men do not regard love-making as a labour which it would be stupid to undertake under circumstances which cannot lead to the production of offspring. A wasp which elaborately seals up an empty nest may be guilty of self-indulgence, but it is scarcely fair that it should be accused of stupidity by a member of a species which has made a fine art of the enjoyment of its instinctive activities divorced from their proper biological consequences." This chapter, stemming from a discussion of Whitehead's theory (in which the words experience and feeling are used for such an elementary physical event as an electronic vibration) will be the greatest hurdle for the non-philosophical reader. Part of the difficulty is unavoidable in this type of literature, in that concepts are more numerous than words, and the reader stumbles along never quite sure whether he is adequately divorcing himself from old connotations, and "translating" the words into the proper strange and new ideas. The section closes with the arguments for panpsychism, the notion that all nature is basically psychical, and that every physical phenomenon is a rudimentary mental process as well. The subject of activity is continued in Chaper IV, "Animal Behavior in Terms of Perception," where the emphasis swings from phi-

[1] Agar, W. E. 1952 (not 1951). A contribution to the theory of the living organism. vi + 235 pp. Victoria, Australia: Melbourne Univ. Press; New York: Cambridge Univ. Press. $3.75.

losophy to psychology and physiology. With perception as the characteristic activity of organisms, the author draws together his knowledge in discussion of tropisms, learning, conditioned reflexes, habituation, and similar phenomena.

Temporal phenomena logically segregate into: considerations of ontogenetic characteristics of the individual (V, Embryonic Development); and long-term changes in the race (VI, Evolution). Professor Agar surveys a considerable area of invertebrate morphogenesis, involving many transplant studies at different periods of maturity. He leads the reader very persuasively along lines of thought that indicate that various "agents" and "sub-agents" are operative, possessing behavior patterns of the same fundamental nature as those of the mature conscious single individual. The final chapter on evolution accepts an interpretation by natural selection of random variations. It then proceeds to investigate the possibility of postulating a directing factor extending through time for the race (a single "subject" in this instance), comparable to the purposiveness exhibited by individual organisms. In the course of this consideration, several very interesting lines of reasoning are followed, as in the discussion of the extreme but orderly modifications that may arise in the case of plant galls. When discussing Lamarkianism, his freedom from bias in following a philosophic lead is admirable: ". . . we will therefore confine ourselves to the question of how far the Lamarkian factor would be useful as an explanatory principle in evolution, assuming that it occurs." After interesting considerations, and recognizing that "the confirmable experiment may yet be forthcoming," he finally concludes "that its value in this direction would be small" (always assuming that Lamarkian inheritance does in fact occur). In short, he finds that the doctrine of the inheritance of acquired characteristics is not only unnecessary, but possibly in conflict with the facts of evolution.

In his final sentence, the author pauses as it were on the brink of another philosophic world, and without once entering it or involving it in the objectivity of the preceding scientific volume, he flings us a challenging glimpse: "It is indeed natural to see in the purposiveness of finite agents a manifestation of a cosmic teleology. Although we have found no necessity to postulate such a factor operating as a directive cause of gene mutation or other heritable variations, this does not exclude a cosmic teleology manifested in the appearance of living organisms in a world capable of supporting them. If, however, the existence of finite purposive agents is to be used as a part of an argument for cosmic teleology, then it follows that this involves an Agent who ensures that the world proceeds to his preconceived goal. As stated earlier, however, a discussion of this would be outside the scope of this book."

Although the "striking features of the present world order" and the progression to a preconceived cosmic goal are legitimate philosophic outlooks, our egos may be sadly deflated when we realize that it would not be our private conscious hormic goals that are of cosmic significance, but the uncomprehended biological consequences.

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A New Omnium Gatherum of Paleozoology[1]

The first great compendium of paleontology was Zittel's *Handbuch der Paläontologie,* in five stout volumes published between 1876 and 1893, with later editions and several translations into French and English. This quickly became the *vade mecum* of generations of paleontologists and the standard reference for all others who needed authentic information on fossil predecessors of living organisms. Paleontology has not been behind the other sciences in its advances during the years since the last editions of Zittel appeared, and its practitioners have yearned for some stout-hearted soul to essay a modern successor.

Three handsome, heavy, volumes of a *Traité de Paleontologie,* edited by Jean Piveteau, formerly of l'École des Mines and now of the Sorbonne, the first of a total of seven, cover the invertebrates and represent a mighty French effort to produce such a successor. A combined operation by some 25 specialists has been required to delineate the present state of systematic paleontology where the tireless pen of Karl von Zittel and three collaborators once sufficed. The over-all impression of the result is the same now as it was some 54 years ago when F. A. Bather remarked of Eastman's English "translation" (with revisions by 12 other authorities) of Zittel:

"The defects in form and arrangement shown by this volume must be a source of regret to all who believe that a good book covering the whole field of systematic zoology cannot nowadays be written without the co-operation of specialists. To attain success, an editor is required to be honey-tongued enough to get all he wants out of his helpers, strong enough to subordinate them to the scheme of the book, and with grasp enough to weld their contributions into a consistent whole." (*Science,* xi, p. 983.)

The *Traité's* editor, and his able coadjutor, Colette Dechaseaux, certainly hoped to avert such a condition, but they have not been able to avoid a good deal of unevenness which is perhaps the most obvious weakness, a weakness which at the same time constitutes a trap for the unwary. There is a marked lack of continuity from phylum to phylum, and within phyla, some groups are thoroughly analyzed by expert hands, and others are clearly the work of some less expert "authorities." There evidently was no firm editorial policy on such things as treatment of systematic categories,—familial names are gallicized in places, latinized in others, for instance. Absence of a name from the indexes is not a certain indication that it is not treated in the text.

[1] **Traité de Paléontologie,** edited by Jean Piveteau. Paris, Masson et Cie. **Tome I** (1952), Les stades inférieures d'organisation du règne animal: Introduction, Generalités, Protistes, Spongiaires, Coelentérés, Bryozoaires; 782 pp., 39 pls., 10 tables, 959 figs. Paper, 8300 f., cloth, 8900 f. **Tome II** (1952), Brachiopodes, Chétognathes, Annélides, Mollusques: 790 pp., 50 pls., 5 tables, 786 figs. Paper, 9000 f., clogth, 9700 f. **Tome III** (1953), Onychophores, Arthropodes, Échinodermes, Stomocordés: 1063 pp., 15 pls., 4 tables, 1269 figs. [Price not indicated].

The only direct contribution by Piveteau to the first three volumes are in introductory, historical chapters in the first volume on the science of paleontology and a brief analysis of the edrioasteroids in the third, but as he is a vertebrate paleontologist, the full weight of his work will undoubtedly be felt in the remaining four volumes. Other introductory parts deal with fossilization, by Jean Roger, principles of systematics, by H. Tintant, this last emphasizing the problems of the living versus the fossil species concepts, with a brief précis of the rules of nomenclature. The latter, however, are evidently not too well known to some of the other contributors. There follow short chapters on chronology and ecology by Colette Dechaseaux, and on phylogenesis of the animal kingdom by the late Lucien Cuénot.

The systematic treatment of the various major groups follows the traditional pattern beginning with unicellular animals, except that the protozoans are included in a kingdom Protista, between the plants and metazoans, in order to include a number of one-celled organisms bordering on plants and animals. Here, Georges Deflandre recognizes two phyla, Rhizoflagellata and Ciliata, with fossil representatives to the subphylum Flagellata of the chrysomonadines, silicoflagellates, coccolithophores, dinoflagellates, ebriedines, euglenians, and phytomonads. In the subphylum Rhizopoda, the Foraminifera are dealt with by Jacques Sigal in a lengthy but superior chapter, wherein practically all genera are mentioned but rather indifferently illustrated. Sigal's concluding section on the eology and paleoecology of Foraminifera is excellent and the most comprehensive for any group in these volumes. Deflandre concludes with the Radiolaria, Ciliata, and those curious groups the hystrichosphaerids and chitinozoans, whose relationships are anyone's guess but whose stratigraphic value is becoming more and more appreciated.

The first of the metazoan phyla, the sponges, is done rather superficially by Leon Moret (Toulouse), with an antiquated classification in which the archaeocyathids are still included, and with no apparent attempt at even a listing of the known fossil genera. It is one of the more disappointing sections of the *Traité*.

Most of the remainder (nearly half) on the first volume is occupied by the coelenterates, edited by James Alloiteau (Sorbonne). He is evidently out of his depth in all of the coelenterate groups except the scleractinians, and nowhere in his contributions is there any overall synthesis of the classification of the phylum, nor a single chart or table showing the geological ranges, evolution, or presumed relationships, of any of the groups treated. The important, extinct Stromatoporoidea are weakly treated and inadequately figured, as are also the other hydrozoans and the scyphozoans. The fossil anthozoans, of course, have the largest paleontological record, and they are rather fully dealt with. The Rugosa and Tabulata, by Marius Lecompte (Belgium), are well and quite thoroughly treated, with good tables of stratigraphic distribution, and it is gratifying to find Lecompte following the growing tendency towards a rational classification of the "tetracorals" based on septal structure. Alloiteau has attempted a through analysis of the scleractinians, his special field, which are referred to only as "Madréporaires Post-Paléozoiques," but it is poorly organized and evidently hastily thrown together from an as-yet-unpublished systematic monograph of the suborder, based on that recently developed by Vaughan and Wells, with some curious departures. Most disturbing to the systematist, perhaps, and overlooking serious omissions, is the reckless manner in which new superfamilies, families, subfamilies, and even genera, are introduced here for the first time. Of 109 subordinal to subfamilial names, 58 are new, and 22 of these are incorrectly formed. There are no less than 65 new genera, mostly dated "1950" or "1951," but actually previously unpublished, and many of them are invalid taxonomically. The illustrations are fair, but many figures chosen for the expensive full-tone plates are of worn or unsatisfactory specimens. There is nothing on the ecology, distribution in time and space, or evolution of the "hexacorals."

One is surprised to find the Bryozoa, Brachiopoda, and Chaetognatha forced together in a phylum "vermidiens." The Bryozoa are cursorily treated by Émile Buge, with only the scantiest analysis of morphology and structure. The classification is essentially that of Bassler, 1934, and only a relatively few genera are even mentioned. This superficial treatment is scarcely relieved by a good discussion of the ecology and associations of the group.

Tome II continues the vermidiens with a lengthy section of the brachiopods by Jean Roger and a page on chaetognaths. If complete coverage of the brachiopods was intended, it falls somewhat short, especially for the articulates. The classification is an uneasy combination of Cooper's provisional and admittedly artificial grouping of 1944, and the older ones of Beecher and Schuchert. Only the briefest notes are given on ecology and phylogeny.

Roger also contributed most of the parts on the phylum Annelida: chaetopods (with which he associates the still-problematical conodonts), hirudinians, and other groups virtually unknown paleontologically.

The Mollusca are introduced by Colette Dechaseaux with brief sections on the Amphineura and Scaphopoda, and a little more than 100 pages on the Pelecyopoda, in which the only bright spots are the 40-odd pages on the rudists and Gabriel Lucas' (Alger) study of the microscopy of the pelecypod shell. Otherwise the coverage is very incomplete and the classification, based largely on hinge structure, will give neontologists some grounds for feeling that paleontology is not really the zoology of extinct organisms, especially when they notice that the phylogenetic classification sketched on page 229 is not followed in the systematic part farther on. It is disappointing to find so little mention of Barrande's host of "Bohemian" pelecypods, as *Panenka* (at least it is not indexed, and thumbing through the pages fails to reveal its mention.)

Nor will the faces of neontologists and paleontologists brighten up when they come next to Geneviève and Henri Termier's (Alger) lick and a promise on the Gastropoda, with a classification still farther removed from reality, and poor illustrations that do no justice to the beautiful shells of these animals.

A little less than half of Tome II is devoted to the Cephalopoda, all of it, with the exception of a short section on the goniatites by G. Delépine (Lille) and another on the dibranchs by J. Roger, by Éliane Basse. Her treatment of morphology, general characters, ecology and evolution is especially well done and summarizes well modern views. The classification of the nautiloids follows that sketched out in 1950 by Flower and Kummel, that of the ammonoids is an attempt to synthesize from the work of Arkell, Spath, Diener, and other great ammonologists. Twenty-four fulltone plates illustrate more than 250 genera.

Tome III completes the invertebrates with the Onychophora, Arthropoda, Echinodermata, and Stomocorda —"les formes ultimes d'invertébrés." Colette Dechaseaux

deals briefly with the first of these. The arthropods are introduced by Gérard Waterlot (Lille), with a classification following that used by Vandel in the *Traité de Zoologie* (1949): trilobitomorphs, chelicerates, and antennates. Under the first the merostomoids, pseudocrustaceans, and marellomorphs, are analyzed by Dechaseaux. Two hundred pages follow on the trilobites by P. Hupé (Sorbonne), with perhaps the most complete treatment of the anatomy, morphology, development, and ecology, yet published. The almost sacred classification of Beecher is finally abandoned and the two orders proposed by Jaeckel, Miomera and Polymera, are revived. Only superfamilies, families, and subfamilies, are diagnosed, genera merely being listed, and only a few are figured. Hupe seems unhappy with the problem of the general evolution of this polyphylogenetic, cryptogenetic, group and it disappointing to find no attempted chart of its evolutionary development.

Under the antennates (mandibulates), Dechaseaux provides brief sections on the branchiopods, so little represented as fossils, copepods, and extinct groups of uncertain position such as *Mimetaster* and *Marria*. The ostracods are ably presented by N. Grekoff, but too briefly considering the paleontologic and stratigraphic importance of the group. Cirripedes are briefly analyzed by H. and G. Termier. The malacostracans, by Jean Roger, are rather thoroughly covered, even including cursory diagnoses of nearly 500 genera, an inequality of treatment thrown in high relief by the brevity of Grekoff's ostracods. Daniel Laurentiaux contributes a suitable chapter on myriadpods and a lengthy one on the insects, for which a symphylian ancestry is regarded as the most satisfactory. The arthropods are completed by two competent chapters on the chelicerates—merostomes and arachnids—by Waterlot.

The echinoderms are introduced by the Termiers. Cuénot has done the heterosteles or carpoids, and the cystoids, unfortunately with nothing on the intriguing relationships of the former. The blastoids and edrioasteroids are uncritically summarized by F. M. Bergouniioux (Toulouse) and Piveteau respectively. The crinoids are dealt with by Georges Ubaghs (Liège) in about 120 pages, 77 of which are concerned with morphology, fairly completely, and ecology and evolution, incompletely, with the result that the systematic exploration is sketchy, and as in the trilobites, descriptive only to the subfamilial level. Many new suborders and superfamilies are proposed. Ubaghs has also done an excellent job on the stelleroids and the problematical ophiocystoids, but this standard is not maintained either in text or figures by the Termiers for the echinoids. The phylum is completed by a brief section on the paleontologically poorly known holothurians by Marthe Deflandre-Rigaud.

Dawydoff's phylum Stomochorda (enteropneusts and pterobranchs) is accepted for the *Traité* as intermediate between the echinoderms and the vertebrates, and here the pterobranchs and graptolites are placed as separate classes by Waterlot, whose treatment of the latter is perhaps a little too short considering the great paleontologic and stratigraphic significance of this extinct group.

Three small groups of uncertain affinities bring us to the end of Tome III: machaeridians (cirripeds, echinoderms, molluscs, or worms?), conulariids (pteropods, hydromedusae, or stomochordates?), and *Hyolithes* and tentaculites, all reviewed by the Termiers.

In spite of its great unevenness and other serious defects, this is a monumental work worthy of great respect, although it is probably less satisfying than Zittel's *Handbuch* was in its day, and it sets a high standard of achievement and production for others who would try the same thing. The price seems high, although actually only a little more than the equivalent price per page for Zittel 75 years ago (3¾ cents per page verus about 3 cents per page for Zittel), but this is still about three times the price per page of the two recent American texts on invertebrate paleontology, both of which are regarded as very expensive even in these times. It is sad to reflect that so few scientists and even fewer students will be able to afford these three desirable volumes (about $85), or the forthcoming four additional volumes on the vertebrates (about $120 more), and many libraries and institutions will think hard before they order them.

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The Relation of Systematics to Other Fields[1]

A book that relates systematics to other aspects of modern biology has long been needed. With the extension of genetics to include natural populations, with more precise and more adequate knowledge of palentology, and with the development of modern ecology correlating field and laboratory investigations of populations and their adaptations, evolutionary theory has been given a sound background that has stimulated a spurt in its scientific progress since about 1930. Taxonomy was long the major discipline of non-medical biology, but there has been a strong recent tendency to emphasize physiology, embryology, cytology and genetics and to drop academic emphasis upon morphological taxonomy. Unfortunately, the pendulum of scientific interest often swings far from the position of equilibrium, and some biologists have developed a biased prejudice against taxonomic research that has proved to be both shortsighted and harmful to a balanced interdependent development of various techniques in the approach to an understanding of life. At the present time there is a strong trend toward the amalgamation of the subsciences of biology into a coordinated whole. With the recognition of connecting principles, a mutual respect for the various research disciplines should result. However, systematic biology suffers from outworn prejudices. Many of our major universities still refuse to accept a doctoral thesis in taxonomy. This book written by authors with broad biological perspective will do much to raise the prestige of systematic biology and to bring a healthy appreciation by all biologists of the problems and accomplishments of taxonomists. Conversely, the book will do much to broaden the outlook of narrow taxonomists and to show them how the discoveries in other fields are vital to the theory and practice of systematics.

[1] Mayr, E., E. G. Linsley and R. L. Usinger. 1953. Methods and Principles of Systematic Zoology. 328 pp., 45 illus. New York. McGraw-Hill, $6.00.

Ecologists, especially community ecologists and biogeographers, have always been dependent upon sound taxonomy. This interdependence has been so obvious that it is surprising to find unreasonable prejudice against taxonomy among prominent ecologists, but human nature being what it is, there will always be some individuals who attempt to enhance their own egos by a supercritical attitude toward others with whom they are psychologically unidentified. The bridging of the gaps between modern aspects of science will increasingly place such individuals on the defensive.

This book can be used as a text for the advanced undergraduate student and it is hoped that more courses in taxonomy of animals may be initiated in university departments as a result. The research student in systematics will have to go further in the development of some techniques, but he can get useful hints and viewpoints from the book. The practical problems of the systematist are discussed and much valuable advice is given for their solution. But the book by no means stops at this point. It takes up the theoretical problems and builds background for the broad interpretation of systematic order. It is fortunate that the authors include specialists in such diverse groups as birds and insects. From the standpoint of a mature understanding of the lower taxonomic categories, birds are probably the best known of all animal groups. From the standpoint of the occurrence of immense numbers and potential abundance of data, the insects provide tremendous opportunity for investigation. A book that is able to present common principles of procedure and theory for groups at such different stages of scientific analysis can be relied upon to cover the main problems of systematics for other animals and plants. Among the animals, the problems of the taxonomy of asexual organisms are hardly touched. The text will serve well for the student of sexual animals, however, and the principles apply well to sexual plants with the exception of polyploid species. There is a short discussion of asexual categories on page 38, but more questions are asked than are answered.

The book is divided into parts dealing with taxonomic concepts, procedure, and nomenclature. Although the emphasis is on theory in the first part, there is also much theoretical interpretation to be found in the part on procedure. The modern synthesis of nomenclature rules and techniques is more important to the taxonomic specialist than to the general biologist, but it too has numerous theoretical implications.

As probably becomes an undergraduate text, there is less emphasis upon the controversial problems of systematics than upon the well supported conclusions and customs. On the whole, however, the authors have given a fine summary treatment of the history and resolution of past controversies. To the reviewer, the most serious fault in the book concerns the definition of the category of the species. The species is probably the key concept of taxonomy and is also a fundamental concept for all theoretical biology. It is not adequately stated in the book that important differences of opinion exist among modern systematists and biologists on this matter and some confusions in the discussion would have been clarified by a more balanced treatment of the species concept. The authors correctly emphasize the role of reproductive isolation as the dividing factor in the Phylogenetic tree. They also make it clear that their concept of the species includes intrinsic reproductive isolation only. Some modern students of the species problem believe that the fundamental dividing factor is the cessation of horizontal gene exchange between existing populations. From the standpoint of basic evolutionary dynamics, extrinsic as well as intrinsic reproductive isolation seems to be an essential factor in speciation. Geographic and ecologic isolation may thus be used along with physiologic, genetic and ethologic isolation in defining the species. The other essential criteria of the species concept are dynamic change, genetic divergence, and the population system. The species may be defined as "an evolved or evolving, genetically distinctive, reproductively isolated, natural population." This definition is merely a brief incorporation of the most generally accepted and applied concepts of the species in the light of modern biology. All of these criteria are necessary, and they emphasize the most important general factors in the process of evolution and speciation. Extrinsic reproductive isolation together with natural selection may be expected to result ultimately in intrinsic isolation as has been pointed out particularly by Muller. Therefore, it is a common observation that the large majority of recognized species of animals and plants are intrinsically reproductively isolated. But there are a small percentage of populations that are not intrinsicially isolated, have no further exchange of genes, are geographically or ecologically prevented from interbreeding and have evolved distinctive taxonomic characters. When the data indicate that no gene exchange between distinctive natural populations occurs, the reviewer would refer such populations to full species, while the authors of the book would refer them to subspecies if they thought that the populations would fuse when and if the extrinsic barriers were broken down. The "potential" ability to interbreed under natural conditions is very difficult to ascertain in allopatric populations and, in addition, the type of isolating mechanism is of less evolutionary importance than the actual cessation of gene flow between diverging populations. Genetic similarity and divergence are the basis for essential taxonomic characters. It is very unfortunate that convergent analogy is ever allowed to be substituted for genetic homology in determining systematic relationships. Confusion on these different principles is the source of much taxonomic error and this confusion is not resolved on page 32. In an advanced treatise on modern systematics, such questions should receive a fuller treatment and evaluation, and it is for this reason that the reviewer considers the book more fitting as an undergraduate text than as an adequate reference work for the research taxonomist.

The book as a whole is so excellent and well organized, and it exhibits such broad biological perspectives, that the reviewer intends to use it in his classes in Field Zoology. A notable forward step in the academic presentation of systematic zoology has been achieved through the publication of this text.

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Fishery Science[1]

The diversity of the material included in this book is at once its strength and its weakness. Almost anyone professionally interested in sport or commercial fisheries will find much that is useful to him: administrator, biologist, economist, engineer, fish-culturist and fisherman. Without being oversimplied or "popular," most of the book is written in non-technical language. Descriptions of kinds of fishing gear, the place of artificial propogation, how to tag fish and why, methods of estimating a fish's age, the effects of regulations upon fish stocks, detection and effects of pollution, pond construction and management, coarse-fish control, fishway construction, collection and use of fishery statistics, etc.—these are all comprehensible to the interested layman, and are accompanied by an abundance of excellent illustrations.

For the fishery biologists the book is a guide to the tools and techniques of his profession. Detailed analytic procedures are given in several all-too-brief chapters which can be recognized by the abundance of formulae. Criteria for separating populations are presented in Chapter 4, methods of estimating population size and mortality rates in Chapters 5 and 6, and mathematical representations and interpretation of data on growth in Chapter 19. These features make the book a required text for the advanced student of Fishery Biology, whether intramural or on-the-job. His complaint will be that more worked examples would have been helpful, but he will have a well-selected list of references for supplementary study.

There is a good index, a glossary, and a list of fishery journals in an appendix.

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[1] Rounsefell, G. A., and W. H. Everhart. 1953. Fishery science: its methods and applications. xi + 444 pp., illus. New York; John Wiley & Sons, Inc. $7.50.

How Animals Move[1]

This delightful little volume, representing the substance of six lectures delivered to a juvenile audience at the Royal Institution, tells one briefly and clearly how animals swim, walk, run, jump, creep, and fly. The author, Dr. James Gray, is well known for his imaginative and penetrating studies on animal locomotion. That he has been able to distill some of the highlights of his own research, as well as that of his colleagues, and present the distillate so simply and in such an entertaining manner is very much to his credit.

An initial chapter dealing in generalized fashion with the "machinery of animal movement" is followed by five chapters, each devoted to some phase of animal locomotion such as swimming, walking and running, jumping and creeping, flying and flapping. The dynamics of each type of animal movement are outlined and are frequently illustrated with drawings of cleverly constructed mechanical models, as well as with action photographs. Morphological adaptations for each type of movement are briefly discussed and examples, chosen largely from the vertebrates, are frequently given. Anyone, old or young, with or without a biological background, who is interested in how animals move about, will derive from a reading of this little volume not only a considerable amount of pleasure but will develop a real understanding of some of the basic principles involved in animal locomotion.

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[1] Gray, James. 1953. How animals move. vi + 114 pp., illus. New York: Cambridge University Press. $3.00.